UNIVERSITÉ DU QUÉBEC À MONTRÉAL

INFLUENCE DE LA COMPOSITION FORESTIÈRE SUR LA SÉQUESTRATION DU CARBONE DANS LES SOLS DU BOUCLIER BORÉAL

THÈSE
PRÉSENTÉE
COMME EXIGENCE PARTIELLE
DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

JÉRÔME LAGANIÈRE

OCTOBRE 2011

À ceux et celles qui se nourrissent de carbone.

REMERCIEMENTS

J'aimerais tout d'abord remercier David Paré, mon superviseur, pour sa confiance, son originalité et pour toute la liberté qu'il m'a offerte au cours de ces années de recherche. Ce fut un grand plaisir de travailler avec David et j'espère que l'occasion se représentera à nouveau. Je remercie également mon co-superviseur, Yves Bergeron, pour sa confiance et pour la qualité de ses conseils. Que ce soit à partir des contrées lointaines abitibiennes ou des côtes méditerranéennes de Montpellier, il a toujours eu un œil attentif sur mes travaux, et ce, malgré la masse d'étudiants qu'il s'inflige. Je suis très reconnaissant envers Denis Angers du Centre de recherche et de développement sur les sols et les grandes cultures (CRDSGC) pour m'avoir accueilli dans son laboratoire, pour sa grande confiance et pour tous ses conseils qui m'ont aidé dans mes activités de recherche et qui m'aideront pour la suite. Je désire aussi remercier chaleureusement Robert Chabot de l'UQAR qui m'a stimulé intellectuellement tout au long de mes études de baccalauréat et dont l'art de travailler m'a tant inspiré qu'il a certes indirectement contribué au succès de la présente thèse.

Je tiens à souligner la contribution des chercheurs impliqués dans le projet stratégique CRSNG dans lequel mon projet de doctorat s'est inscrit : Han Chen, Xavier Cavard, Brian Brassard, Triin Ilison, Stephen Hart, Meelis Seedre, Anthony Taylor, Dominic Lafontaine-Senici et Sonia Légaré. J'aimerais remercier Michelle Bernier-Cardou pour ses conseils en statistiques ainsi que Pamela Cheers et Isabelle Lamarre pour leur aide précieuse dans la correction et l'édition de mes manuscrits. Je remercie aussi mon collègue du Centre de foresterie des Laurentides (CFL) et ami, Luc St-Antoine, pour son support technique journalier et sa grande qualité humaine. Un grand merci à Marie-Hélène Longpré, Jessie Parent, Éric Girard, Jessica Lagacé-Banville, Alain Courcelles, Serge Rousseau, Gabriel Lévesque et Johanne Tremblay pour leur aide exceptionnelle effectuée au terrain et au laboratoire.

Je remercie sincèrement mes collègues de l'UQÀM, de l'Institut des sciences de l'environnement, du Centre d'étude de la forêt, du CFL et du CRDSGC pour ces belles années passées en leur compagnie. Je remercie ma soeur Virginie pour ses encouragements et pour son sofa-lit suédois qui m'a été très utile lors de mes séjours à Montréal. Merci à mes parents, Jean-Luc et Michelle, pour m'avoir inculqué des valeurs comme la persévérance, l'originalité, l'humilité et la remise en question. Ce cocktail de qualités est, pour moi, essentiel à la réalisation d'un chercheur. Enfin, un merci tout spécial à ma bien-aimée Thalia, sans qui l'accomplissement de ce grand projet n'aurait pas été simple. Merci pour tes encouragements, ton intérêt, ta patience et ta confiance, sans oublier le congé de tâches ménagères pendant les derniers mois de rédaction. Merci d'être là.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

Les forêts du Bouclier boréal stockent de grandes quantités de carbone (C) sous forme de C organique du sol (COS). Toutefois, l'intégrité de ces stocks de COS est menacée par les changements climatiques, mais aussi par la modification de la composition forestière à l'échelle du paysage. En effet, chaque espèce d'arbre possède des traits fonctionnels différents lui permettant d'avoir une influence singulière sur son environnement et sur des processus comme l'accumulation, le stockage et la libération du COS. L'acquisition de connaissances sur la dynamique du COS en forêt boréale est fondamentale pour prédire et atténuer les conséquences de tels changements. L'objectif de cette thèse était d'explorer l'influence de la composition forestière (1) sur la quantité, la distribution et la qualité du COS et sa stabilité face au réchauffement, (2) sur la répartition du COS dans des fractions physiques de sol qui varient en stabilité, et (3) sur les pertes annuelles de CO_2 *in situ* et les facteurs responsables de la variation entre les types de forêts.

Collectivement, les résultats montrent que la composition forestière affecte grandement la dynamique du COS en forêt boréale. L'influence de la composition forestière sur les pertes de CO_2 se faisait surtout via des variations dans la température du sol et dans la qualité biochimique du C produit dans les types de forêts étudiées. En général, les forêts contenant du peuplier faux-tremble accumulaient moins de COS en surface que les forêts contenant des conifères (pin gris et épinette noire), mais il y en avait davantage en profondeur, endroit où le C est moins susceptible d'être libéré dans l'atmosphère et donc plus stable. Les forêts contenant du peuplier avaient aussi davantage de COS situé dans les fractions physiques du sol les plus stables, c'est-à-dire celles étroitement associées aux particules minérales. Bien que les forêts d'épinettes noires soient celles qui possédaient la plus grande quantité de COS de surface de tous les types de forêts étudiées, ce COS était le plus sensible à l'augmentation de la température de sorte que sa réponse au réchauffement se traduisait par une libération de CO_2 plus élevée. De plus, comme le stock de COS de surface des conifères est en partie liée à un microclimat du sol plus froid induit par le peuplement, la libération du CO_2 suite à des perturbations qui ouvriraient le couvert ou en changeraient la composition pourrait être plus importante que dans les forêts de feuillus. En conclusion, les résultats de cette thèse suggèrent que le rajeunissement des forêts et notamment l'augmentation du couvert de peuplier faux-tremble dans le paysage diminuerait la taille des stocks de COS, mais en augmenterait la stabilité. Par ailleurs, les forêts d'épinettes noires, qui possèdent d'importants stocks de COS et qui dominent la forêt boréale canadienne, pourraient perdre de grandes quantités de COS suite au réchauffement du climat ou à une transformation du couvert.

Mots clés : forêt boréale, composition forestière, séquestration du carbone, matière organique du sol, changements climatiques

INTRODUCTION

La forêt boréale séquestre une grande quantité de carbone (C) dans la végétation et le sol, faisant de cet écosystème l'un des plus grands réservoirs de C, principalement sous la forme de C organique du sol (COS) (Lorenz et Lal 2010). La taille du réservoir de COS est fonction de l'équilibre entre les gains de C provenant de la chute de litière, aérienne (p.ex. feuilles, branches, fructifications) et sous-terraine (p.ex. racines), et les pertes de C sous forme de CO_2 provenant de la respiration microbienne au cours de la décomposition de la matière organique du sol (MOS) et des perturbations comme les feux de forêts (Schimel et al. 2000; Schimel et al. 2001; Chen et al. 2002). Plusieurs facteurs influencent les entrées et les sorties de C dans le sous-système du sol. Par exemple, des facteurs climatiques comme la température et les précipitations peuvent affecter la productivité primaire nette et donc la quantité de C retourné au sol sous forme de litière, mais également l'activité des micro-organismes décomposeurs et la quantité de C libéré dans l'atmosphère (Lorenz et Lal 2010). La qualité de la litière, c.-à-d. sa composition biochimique, qui est notamment déterminé par les traits fonctionnels des espèces qui la produisent, va influencer la vitesse à laquelle les micro-organismes décomposent cette MOS et libèrent le C (Berg 2000; Trofymow et al. 2002).

Le destin du COS est de se faire respirer par les micro-organismes pendant la décomposition. Le temps de résidence du C entrant dans le sous-système du sol est hautement variable, demeurant de quelques jours seulement à plusieurs centaines d'années dans le sol (von Lützow et al. 2006). La séquestration à long-terme est possible lorsque des mécanismes de stabilisation du C interviennent. Parmi ces mécanismes qui réduisent ou même empêchent l'utilisation du C par les micro-organismes, figurent les contraintes climatiques, la protection physico-chimique à l'intérieur des agrégats de sol et la protection biochimique, aussi appelée récalcitrance (Davidson et Janssens 2006; von Lützow et al. 2006). Les contraintes

climatiques s'observent généralement dans des conditions extrêmes de température (p.ex. pergélisol), d'humidité (p.ex. sécheresse) ou d'oxygénation (p.ex. conditions anaérobiques) et peuvent réduire de façon importante l'activité microbienne jusqu'à l'empêcher (Davidson et Janssens 2006). La formation d'agrégats stables est possible lorsque la matière organique et les particules minérales s'agglomèrent sous l'action des micro-organismes et de la faune du sol (Tisdall et Oades 1982; Six et al. 2004). Des liens chimiques stables à la surface des particules minérales fines sont alors créés par adsorption (protection chimique) en plus de l'occlusion par agrégation qui réduit l'accessibilité spatiale du C aux micro-organismes et à leurs enzymes (protection physique) (von Lützow et al. 2006; Jastrow et al. 2007). La récalcitrance, quant à elle, réfère à la composition biochimique de la matière organique (initiale ou altérée par les micro-organismes ou le feu) et plus précisément à la présence de composés complexes résistant à la dégradation (p.ex. lignine, polyphénols comme les tanins, lipides, cires, produits de dégradation microbienne) (Trofymow et al. 2002; von Lützow et al. 2006). Tous ces mécanismes de stabilisation du COS s'observeraient à différents degrés dans les sols forestiers et varieraient notamment en fonction de la composition forestière, mais peu d'études s'y sont attardées (Lorenz et Lal 2010).

En effet, chaque espèce d'arbre possède des traits fonctionnels différents qui lui permettent d'avoir une influence singulière sur son environnement dont le sol dans lequel elle croît. Par exemple, suivant des différences dans la tolérance à l'ombre, la persistance du feuillage (feuilles persistantes vs. caduques), la capacité d'évapotranspiration, et la composition de la strate herbacée (p.ex. présence de bryophytes), les conditions d'humidité et de température au sol peuvent varier en fonction du type de peuplement (Binkley 1995; Abu-Hamdeh et Reeder 2000; Amiro et al. 2006; Hart et Chen 2006; Hobbie et al. 2006). Par ailleurs, la litière produite par différentes espèces d'arbres et leurs communautés végétales associées contiennent différentes proportions d'éléments nutritifs et de composés récalcitrants qui déterminent la vitesse à laquelle le COS se décompose (Berg 2000; Preston et al. 2000). Les espèces qui produisent des litières acides peuvent même empêcher la présence de macro-invertébrés comme les vers de terre qui sont reconnus pour accélérer la décomposition du COS en surface et favoriser la formation et la stabilisation d'agrégats de sol (Bossuyt et al. 2005; Reich et al. 2005; Laganière et al. 2009). Autrement, la morphologie du système

racinaire varie selon les espèces et influencerait le patron de distribution du COS dans le profil de sol (Strong et La Roi 1983; Brassard et al. 2011). Par conséquent, en générant des conditions microclimatiques particulières, en fournissant un apport en C sous forme de litière variant en qualité et en quantité, en influençant la distribution verticale du COS dans le profil de sol, et aussi en influençant le degré de protection du COS dans le sol minéral, les espèces d'arbres auraient la capacité d'influencer l'accumulation, le stockage et la libération du COS.

Mis à part l'influence qu'une espèce d'arbre seule peut avoir sur son environnement, le mélange de deux ou plusieurs espèces d'arbres en peuplements mixtes pourrait avoir des effets non additifs (synergique ou antagoniste) sur la séquestration du COS. L'hypothèse de séparation de niche veut qu'un peuplement mixte composé d'espèces possédant des traits fonctionnels complémentaires (divergents) puisse maximiser l'utilisation des ressources disponibles (lumière, eau et nutriments) et ainsi permettre une productivité primaire nette supérieure à celle des monocultures de chaque espèce compagne (Hooper et al. 2005; Kelty 2006). Toutefois, la majorité des études ayant testé cette hypothèse se sont déroulées en milieu non forestier, dans des écosystèmes de prairies (Hooper et al. 2005). Pourtant, plusieurs essences communes dans le paysage canadien comme le peuplier faux-tremble (*Populus tremuloides* Michx.), l'épinette noire (*Picea mariana* (Mill.) BSP) et le pin gris (*Pinus banksiana* Lamb.) possèdent des traits fonctionnels différents et minimiseraient la compétition en mixité (Figure 0.1). L'occurrence de ces essences en peuplements mixtes pourrait se traduire par un gain de productivité primaire nette et signifierait une augmentation des apports de C retourné au sol dans les forêts mixtes comparativement aux forêts pures.

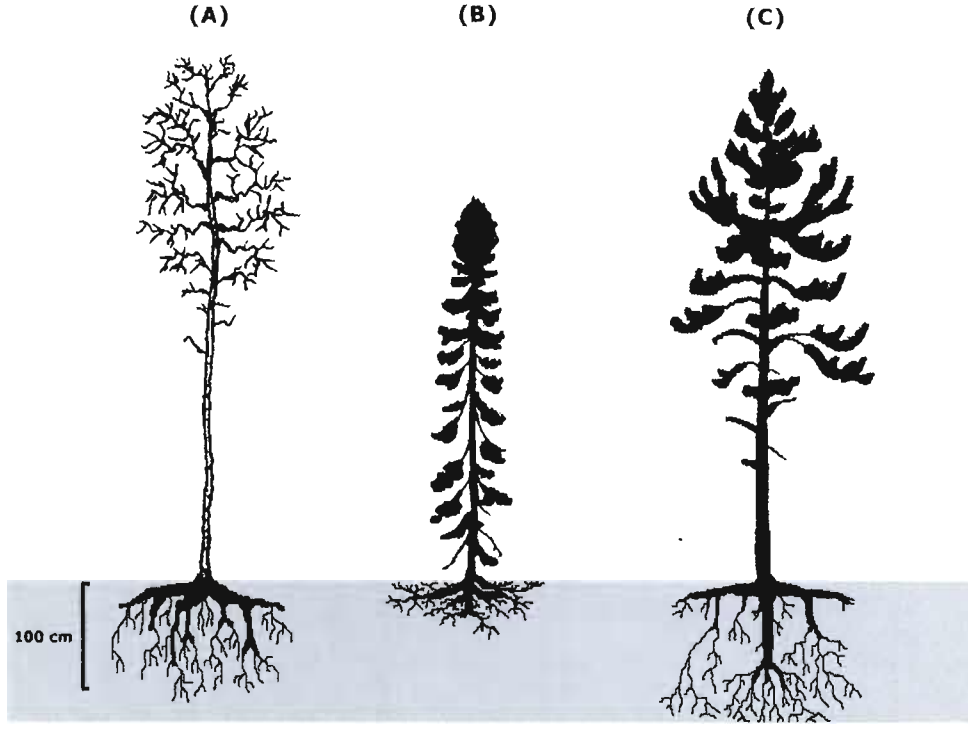

Figure 0.1 Schéma approximatif illustrant la différence de traits fonctionnels entre (A) le peuplier faux-tremble, (B) l'épinette noire et (C) le pin gris, notamment au niveau de l'utilisation des ressources sous-terraines (eau et nutriments) et aérienne (lumière) dans l'espace, mais aussi dans le temps (c.-à-d. feuillages persistants vs. caducs). Le peuplier faux-tremble est un feuillu intolérant à l'ombre qui possède un système racinaire profond permettant d'aller chercher l'eau et les éléments nutritifs en profondeur. À l'opposé, l'épinette noire est un conifère tolérant à l'ombre, à feuilles persistantes, qui possèdent un système racinaire superficiel. Le pin gris est également un arbre à feuilles persistantes, mais qui est intolérant à l'ombre et dont le système racinaire se compose d'un pivot s'ancrant très profondément dans le sol (Strong et La Roi 1983; Sims et al. 1990).

Autrement, une hypothèse plus étudiée en milieu forestier pourrait également expliquer un effet non additif sur la séquestration du COS. L'hypothèse de facilitation veut que la présence d'une espèce puisse améliorer les conditions de croissance d'une autre espèce (Man et Lieffers 1999; Hooper et al. 2005; Kelty 2006). Par exemple, la litière de feuilles d'une espèce présente dans un peuplement pourrait améliorer les propriétés du sol de tout le peuplement et pourrait non seulement accélérer la minéralisation des éléments nutritifs et

stimuler la productivité du peuplement, mais également accélérer la décomposition et ainsi réduire les stocks de COS (Man et Lieffers 1999; Gartner et Cardon 2004; Hättenschwiler et al. 2005). L'effet facilitatif du peuplier faux-tremble sur les conditions de sol de l'épinette noire est bien documenté (Légaré et al. 2005b; Laganière et al. 2009, 2010b). Somme toute, la littérature traitant du rôle joué par les forêts mixtes en terme de séquestration de carbone est pratiquement inexistante et requiert plus d'attention, notamment lorsque l'aménagement a pour objectif d'accroître la séquestration du C par la promotion de plantations mixtes (Jandl et al. 2007; Paquette et Messier 2011).

Dans le Bouclier boréal du Canada (Figure 0.2), l'épinette noire est l'espèce d'arbre la plus commune, couvrant plus de 60 millions d'hectares (Canada's NFI 2010). Les peuplements d'épinette noire accumulent de grandes quantités de COS, notamment à cause de la faible qualité des apports en C et des conditions micro-environnementales limitant les taux de décomposition du COS (Fenton et al. 2005; Lavoie et al. 2005; Laganière et al. 2009). Au cours du siècle passé, de vastes superficies de conifères ont fait place à des forêts de feuillus, comme le peuplier faux-tremble, en réponse à un changement dans la taille et la fréquence des perturbations comme les coupes forestières, les épidémies d'insectes et les feux de forêt (Bond-Lamberty et al. 2007; Soja et al. 2007; Ilisson et Chen 2009b; Laquerre et al. 2009). De récentes études ont montré que la présence de peuplier faux-tremble dans des peuplements dominés par l'épinette noire était associée à une litière de meilleure qualité et une amélioration des conditions microclimatiques du sol, menant à une augmentation de l'activité microbienne et un accroissement des pertes de COS par décomposition (Légaré et al. 2005b; Laganière et al. 2009, 2010b). En plus du changement dans la composition forestière, les changements climatiques pourraient aussi modifier la dynamique du COS et particulièrement dans les régions nordiques, puisqu'un réchauffement plus important y est anticipé (IPCC 2007). Sachant que les pertes de COS par décomposition augmentent avec la température (Davidson et Janssens 2006), l'intégrité des stocks de COS du Bouclier boréal pourrait être menacée dans le futur s'il n'y a pas de changements dans la qualité et la quantité des apports en C associés avec le réchauffement (Lorenz et Lal 2010). La compréhension du rôle de la composition forestière sur le cycle du C est fondamentale pour accroître notre

capacité à prédire et atténuer les conséquences des changements climatiques et l'impact des modifications de l'écosystème forestier par l'activité humaine.

Figure 0.2 Localisation des deux aires d'études concernées par la présente thèse. Elles font parties de l'écozone du Bouclier boréal qui s'étend sur 1,8 million de kilomètres carrés, du nord de la Saskatchewan à Terre-Neuve (Source : Ressources Naturelles Canada).

Dans cette étude, des peuplements forestiers similaires sous plusieurs aspects (climat, matériau originel, drainage, topographie, âge) ont été sélectionnés dans le but **d'explorer l'influence de la composition forestière du Bouclier boréal sur :**

(1) la quantité, la distribution et la qualité du COS,

(2) la répartition du COS dans les fractions physiques du sol, et,

(3) les pertes annuelles de COS *in situ* et les facteurs responsables de la variation entre les peuplements.

Chacun de ces trois objectifs sera abordé en profondeur dans un chapitre distinct de la présente thèse. Pour réaliser ces objectifs, deux régions d'étude ont été ciblées à travers la forêt boréale canadienne : dans l'Est, soit à la limite supérieure de la région de l'Abitibi-Témiscamingue et Nord-du-Québec dans la province de Québec et, dans le centre, au nord de Thunder Bay dans la province de l'Ontario (Figure 0.2). Des essences forestières communes à chacune de ces régions ont été sélectionnées. Au Québec, des peuplements mixtes et purs de peuplier faux-tremble et d'épinette noire ont été sélectionnés, sur des sols à texture fine (argileux), à raison de 8 réplications pour un total de 24 parcelles. En Ontario, des peuplements mixtes et purs de peuplier faux-tremble et de pin gris ont été sélectionnés sur des sols à texture grossière (loam-sableux), à raison de 5 réplications pour un total de 15 parcelles. Dans la mesure du possible, les parcelles de composition forestière différente ont été réunies en blocs pour tenir compte de la variabilité intersites dans l'analyse des données (sites du Québec seulement). Tous les peuplements se sont régénérés suivant un feu de forêt.

CHAPITRE I

STABILITY OF SOIL CARBON STOCKS VARIES WITH FOREST COMPOSITION IN THE CANADIAN BOREAL BIOME

Dans ce premier chapitre, j'essayerai d'établir que la composition de la forêt influence non seulement la taille des stocks de COS, mais également la distribution verticale et la qualité du COS, de même que sa réponse à l'augmentation de la température au cours d'une expérience d'incubation de sol en conditions contrôlées (en laboratoire). Ce premier chapitre permettra donc d'estimer la quantité de COS (jusqu'à 55 cm de profondeur) présent dans différents types de peuplements de la forêt boréale canadienne et d'en évaluer la stabilité, ce qui n'était pas connu jusqu'à maintenant.

Tous les co-auteurs ont contribué à la conceptualisation et à l'élaboration du design expérimental de l'étude et à la révision du présent article scientifique. JL a exécuté la recherche, analysé les données et écrit l'article. HYHC est le chercheur principal du projet stratégique CRSNG dans lequel mon doctorat s'est inscrit. BWB et XC sont des étudiants au doctorat qui ont réalisés leurs recherches sur les mêmes sites d'étude. La référence de l'article est :

Laganière, J., D. Paré, Y. Bergeron, H.Y.H. Chen, B.W. Brassard et X. Cavard. 2011. Stability of soil carbon stocks varies with forest composition in the Canadian boreal biome. Soumis à Ecosystems.

1.1 Résumé

La composition de la forêt boréale, qui change en réponse à l'aménagement forestier, aux perturbations naturelles et aux changements climatiques, affecterait l'accumulation de carbone organique du sol (COS). Cette étude a exploré l'influence d'espèces d'arbres communes à la forêt boréale (peuplier faux-tremble, épinette noire, pin gris), à la fois en forêts pures ou en mélanges feuillus-conifères, sur la taille, la distribution et la qualité du COS dans deux régions du biome boréal canadien. La qualité du COS a été évaluée en quantifiant les proportions de C rapidement utilisable par les microorganismes (appelé C rapide) et de C actif (appelé CPM) par le biais d'incubations à long terme en laboratoire. Les stocks de COS du profil de sol entier ne différaient pas significativement selon le type de peuplement alors que la distribution et la qualité du COS différaient. En général, les forêts contenant des conifères stockaient principalement le COS en surface alors que les forêts de peuplier le stockaient plutôt en profondeur. Les proportions et les contenus de C rapide et de CPM diminuaient en profondeur, indiquant que le COS est plus stable à cet endroit. Il y avait généralement moins de CPM dans les forêts de peuplier. Nos résultats indiquent que le stock de COS du peuplier était plus stable parce qu'il contenait moins de C actif et parce qu'une plus grande partie était située en profondeur comparativement aux autres types de forêts. Nous avons aussi trouvé que la sensibilité de la décomposition du COS à la température augmentait avec la qualité du C (c.-à-d. la proportion de C rapide) lorsque nous considérions une échelle de températures reflétant les conditions *in situ* (en-dessous de 15°C), suggérant que la réponse des sols nordiques au réchauffement planétaire pourrait être contrôlée par la quantité de COS labile. Notre travail met en évidence qu'un changement dans la composition de la forêt boréale pourrait influencer la stabilité des stocks de COS et, par conséquent, l'effet des changements climatiques sur ce grand réservoir de C.

1.2 Abstract

Boreal forest composition, which changes as a result of forest management, natural disturbances and climate change, may affect the accumulation of soil organic carbon (SOC). This study explored the influence of common boreal tree species (trembling aspen, black spruce and jack pine), either in pure stands or in conifer-broadleaf mixtures, on the amount, distribution and quality of SOC in two regions of the Canadian boreal biome. SOC quality was assessed by quantifying proportions of rapidly-released C (termed fast C) and active C (termed PMC) using long-term laboratory incubations. Stocks of SOC of the whole soil profile did not significantly differ with stand type while distribution and quality did. In general, stands containing conifers stored SOC mostly near the surface while aspen stands stored SOC mostly in deeper layers. Proportions and contents of fast C and PMC decreased with increasing soil depth, thus indicating that deep SOC was more stable. Less PMC was generally found in aspen stands. Our results pointed out that the SOC stock under aspen was more stable because it contained less active C and because a larger part was confined to deep soil layers relative to other stand types. We also found that temperature sensitivity of SOC decomposition increased with C quality (i.e. proportion of fast C) when considering a temperature range commonly experienced in these soils (below 15°C), suggesting that the response of northern soils to global warming might be controlled by the amount of labile SOC. Our work highlights that changes in boreal forest composition could influence the stability of SOC stocks and therefore the effect of climate change on this large C pool.

1.3 Introduction

The boreal forest stores large amounts of C through vegetation and soil, making this biome one of the greatest terrestrial carbon reservoirs, mainly in the form of soil organic C (SOC) (Lorenz and Lal 2010). Accumulation of SOC depends on the balance between C input (e.g. litterfall) and output rates (e.g. decomposition). The residence time of C entering the soil system is highly variable, ranging from a few days to thousands of years (von Lützow et al. 2006). Long-term stabilization of SOC may occur when organic matter is mixed with mineral particles and forms organo-mineral complexes (i.e. soil aggregates), but also when organic matter quality or environmental conditions are unfavourable for microbial decomposition (von Lützow et al. 2006). In the boreal forest, the general poor plant litter quality and low temperatures are responsible for the observable low microbial activity and decomposition rates, allowing SOC to accumulate (De Deyn et.al. 2008).

Across this regional pattern of low-quality litter and cold climate characterizing the boreal biome exists a relatively wide range of organic matter quality and microclimatic conditions that differ in response to forest composition. For example, following different shade tolerance, foliage persistence (i.e. evergreen or deciduous), evapotranspiration capacity (water requirements), and understory composition (e.g. presence of bryophytes), soil microclimatic conditions may be relatively cold and wet under some tree species (e.g. *Abies* sp. and *Picea* sp.) and warmer and drier under other species (e.g. *Betula* sp. and *Populus* sp.), under similar permanent site conditions (Binkley 1995; Hart and Chen 2006; Hobbie et al. 2006). Moreover, the litter produced by each boreal tree species and associated understory contains various proportions of nutrients, lignin and secondary metabolites that determine the quality of litter and rates of decomposition (Berg 2000; Preston et al. 2000). The production of acidic litter can even prevent the presence of macroinvertebrates that may either enhance the breakdown of organic matter, the formation and stabilization of soil aggregates in mineral layers or both (Bossuyt et al. 2005; Reich et al. 2005; Laganière et al. 2009). Otherwise, structural traits such as the shape of the rooting system differ among tree species and may contribute to different patterns of accumulation and stabilization of SOC in the soil profile (Strong and La Roi 1983; Brassard et al. 2011). Therefore, by generating specific soil microclimatic conditions, by producing litter in variable amounts and quality, by influencing

the distribution of SOC within the soil profile, and also by influencing the degree of SOC protection within the mineral soil, tree species have the potential to influence the fate of C in soil.

Alteration of the boreal ecosystem dynamics may have strong implications in terms of climate change concerns and greenhouse gas mitigation efforts. Over the past century, for example, large areas of the boreal forest have been changed from coniferous species into broadleaved species such as trembling aspen (*Populus tremuloides* Michx.) by changes in the size and the frequency of disturbances including forest cutting activities, insect outbreaks and wildfires (Bond-Lamberty et al. 2007; Soja et al. 2007; Ilisson and Chen 2009b). This phenomenon is particularly critical for the maintenance of boreal SOC stocks given that aspen stores less SOC compared with black spruce (*Picea mariana* Mill. BSP) (Laganière et al. 2011), the most widespread tree species in the Canadian boreal forest (Canada's NFI 2010). In addition to changes in forest composition, SOC stocks of the boreal biome might be particularly vulnerable to global warming because a stronger temperature increase is anticipated in northern latitudes compared with the global average (IPCC 2007). Given the inherent temperature dependence of organic matter decomposition, SOC stocks might decrease under climate warming if not compensated for with a greater net primary production or with a decrease in the quality (decomposability) of litter produced (Lorenz and Lal 2010).

Surprisingly, few studies have examined the influence of forest composition on the amount and stability of soil C stocks in boreal forest ecosystems. Yet, a review by Jandl et al. (2007) highlighted the necessity to differentiate SOC into labile and stable fractions among tree species. Owing to a lack of data, the effect of tree species on SOC storage in stable pools is questioned and still insufficiently proven (Jandl et al. 2007). To accurately assess the impacts of recent and future ecosystem changes on the fate of the boreal SOC pool, we need to improve our knowledge of SOC dynamics as affected by forest composition.

The aim of this study was to explore the influence of common boreal tree species (two conifers: black spruce and jack pine *Pinus banksiana* Lamb., one broadleaf: trembling aspen, and conifer - trembling aspen mixtures), on the amount, distribution and quality of SOC in two regions of the Canadian boreal biome. The amount and distribution of SOC were

evaluated by sampling different layers of the soil profile (up to 55 cm depth) for their C contents while the C quality was assessed by quantifying proportions of rapidly-released C (termed "fast C") and active C (termed "potential mineralizable C" or PMC) in these soil samples using long-term laboratory incubations (379 d) at a high temperature (29°C). The temperature sensitivity of SOC decomposition, the so-called Q_{10} (factor by which a process rate increases with a 10° rise in temperature), was also determined by incubating additional soil samples at three temperatures (2, 14 and 29°C). Because permanent site conditions such as climate, soil type and texture, drainage, topography, and time since fire were not related to tree species composition, variations of dependent variables are attributed to the effect of tree species and their associated understory.

1.4 Materials and methods

1.4.1 Study area and sampling

This study was conducted in two regions of the North American boreal forest, Canada. One study region was located in northwestern Ontario (named "ON" hereafter), approximately 150 km north of Thunder Bay (49°23'N to 49°37'N, 89°31'W to 89°45'W). The climate is boreal with a mean annual precipitation (MAP) totalling 712 mm and mean annual temperature (MAT) of 2.5°C (Environment Canada 2010). Five stands dominated by jack pine, five stands dominated by trembling aspen, and five stands mixed uniformly with both tree species were selected in an area of 250 km^2 with a maximum distance of 30 km between sites (total: 15 stands). The understory plant communities typically growing below the forest canopy of a given tree species (i.e. associated understory) and generally consisting in herbs, shrubs and bryophytes were similar within a stand type. The vegetation under jack pine included mainly herbs (*Cornus canadensis* L., *Maianthemum canadense* Desf., and *Linnaea borealis* L.) and feathermosses. The aspen understory included shrubs (*Acer spicatum* Lamb., *Rubus pubescens* Raf., and *Ribes glandulosum* Grauer ex Weber) and herbs (*M. canadense*, *Mitella nuda* L., and *Aster macrophyllus* (L.) Cass.) while the mixedwood understory comprised a mixture of those found under spruce and aspen. Soils were well-drained silty loams to sandy loam classified as Brunisols and originating from glacial till deposits (Soil Classification Working Group 1998), the topography was relatively flat and all stands originated from the same wildfire in 1923 (Senici et al. 2010).

The second region was located in western Quebec (named "QC" hereafter), approximately 50 km northeast of La Sarre (49°08'N to 49°11'N, 78°46'W to 78°53'W). The climate is boreal with a MAP totalling 890 mm and a MAT of 0.7°C (Environment Canada 2010). Eight stands dominated by black spruce, eight stands dominated by trembling aspen, and eight stands mixed uniformly with both tree species were selected in an area of 100 km^2 with a maximum distance of 10 km between sites (total: 24 stands). The vegetation under spruce canopy included mainly herbs (*C. canadensis*, *Rhododendron groenlandicum* (Oeder) Kron and Judd, and *Vaccinium* spp.), and big red stem moss (*Pleurozium schreberi* (Bird.) Mitt.); the latter was the dominant ground cover and an important input of organic matter to the soil (Bisbee et al. 2001). The aspen understory included shrubs (*R. pubescens*, *Diervilla lonicera* Mill., and *Viburnum edule* (Michx.) Raf.) and herbs (*C. canadensis*, *Viola* spp., *L. borealis*, and *M. canadense*) while the mixedwood understory comprised a mixture of those found under spruce and aspen. Soils were moderately-drained silty clays classified as Luvisols and originating from glaciolacustrine deposits (Soil Classification Working Group 1998), the topography was flat and all stands originated from the same wildfire in 1916 (Légaré et al. 2005a).

Similar to other studies that investigate the species mixture effect in naturally established mature stands (e.g. Wang et al. 2002; Cavard et al. 2010; Brassard et al. 2011), and in following the definitions for single- and mixed-species stands in the forest resource inventory, the criteria for stand selection were that mixed-species stands would contain >20% stand basal area of trembling aspen and jack pine (ON region) or black spruce (QC region), while single-species stands would have >80%.

During the selection of the sites, particular attention was given to ensuring the similarity of the following permanent site conditions: climate, soil type and texture, parent material, drainage, topography, and time since fire. Permanent site conditions are site characteristics that affect soil formation and do no vary over a short-time scale. Furthermore, all selected stands were >1 ha in area, fully stocked and visually homogeneous in structure and composition. Thus, any variation in the dependent variables is assumed to be the effect of tree species and their associated understory. More information on stand characteristics is found in Brassard et al. (2011) and Cavard et al. (2010; 2011).

In each stand, a 400 m^2 circular plot was established for soil sampling. The species and the diameter at breast height were determined for all trees >5 cm diameter for estimating tree species basal area (Table 1.1). In June 2006, after complete thawing of the soil, four samples of the entire organic layer (i.e. forest floor or O horizon) were collected using a sharp knife and a trowel in a 15 cm x 15 cm block while four samples of the surface mineral layer (0-15 cm), two samples of the intermediate mineral layer (15-35 cm) and one sample of the deep mineral layer (35-55 cm) were carefully extracted from each plot with a metal corer (diam: 4.7 cm). These samples were pooled by depth to yield composite samples. Similarity of drainage class, parent material and soil type were verified by digging a soil pit (ca. 1 m^3) in each sampling plot (Soil Classification Working Group 1998).

1.4.2 Soil analyses

The field-moist soil was passed through 6- and 4-mm sieves for organic and mineral layers, respectively, before air-drying and weighing to determine soil bulk density according to Carter and Gregorich (2007). Before and after the incubation, subsamples from all soils were ground and analyzed for their C concentrations by dry combustion using a LECO CNS-2000 analyzer (Leco Corp., St. Joseph, MI, USA). No carbonates were detected in soil samples, thus the C analysis was a measure of total organic C concentration (Carter and Gregorich 2007). C contents (in Mg C ha^{-1}) were then calculated by multiplying C concentrations with their respective soil bulk densities and sampling depths. Cation exchange capacity (CEC) was determined by summing exchangeable cations extracted with 0.1 *M* $BaCl_2$ and by atomic-absorption spectrophotometry (Hendershot et al. 2007). The pH was determined in water with a PHM82 pH meter (Radiometer, Copenhagen, Denmark) using a 1:10 and 1:2 soil:water ratio for organic and mineral layers, respectively (Carter and Gregorich 2007). Soil texture was determined using the standard hydrometer method (Kroetsch and Wang 2007).

1.4.3 Microcosm preparation

Organic and mineral layer subsamples corresponding to 6- and 40-g dry weight, respectively, were placed on a layer of glass wool in 120 mL plastic containers (28 cm^2 surface area), wetted at field capacity and placed in 500 mL glass jars (Mason type). These

microcosms were left to equilibrate for one week at 2°C after handling and were then incubated in the laboratory at constant temperature (29°C) and soil moisture (field capacity) during 379 days. Long-term laboratory incubations followed by a modelling procedure is a useful empirical technique that provides an estimate of the proportion of "potential mineralizable C" (PMC) or "active C" present in a soil sample under standard conditions (the remaining proportion of C being considered as stable or passive) by measuring the release of C by microbes over a long period of time (Paré et al. 2006). The use of a high temperature allows the microbial community to mineralize a maximum of active organic material and increases the accuracy of the modeled PMC values (modelling procedure) because the mineralization curves can reach a plateau earlier compared with incubations at low temperatures (Figure 1.5). A temperature between 20-35°C is commonly used to calculate PMC (Zak et al. 1993; Côté et al. 2000; Halpern et al. 2010; Maillard et al. 2010).

An additional incubation experiment was performed to estimate the temperature sensitivity of soil organic matter decomposition (Q_{10}). Three sets of subsamples were created by further pooling replicated soil samples together (by stand types) and the resulting composite subsamples (non-replicated) were incubated at constant temperatures (2, 14 and 29°C) and soil moisture (field capacity) during 379 days. Because previous laboratory incubations at low temperatures have shown very low variability in C mineralization rates among sites (Paré et al. 2006; Rey and Jarvis 2006), we are confident that mineralization curves of soils incubated at 2 and 14°C represent a realistic average of the replicated stand types sampled in this study. Further, examination of Figure 1.5 indicates that mineralization curves from composite subsamples incubated at 29°C are within the error range of that from replicated samples (termed "29°C Rep").

1.4.4 Carbon mineralization measurements

Soil CO_2 effluxes (C mineralization rates) were determined every week for the first four weeks and once a month thereafter (until the end of incubation). During measurements, the Mason jars were closed with airtight lids containing a rubber septum. The first gas sample was taken from the headspace with a syringe immediately after closing and directly injected into a LI-6200 infrared gas analyzer (LI-COR, St. Joseph, MI,.USA) modified to allow us to

measure a small volume of CO_2 (LI-COR, Application Note #121). The measurement was repeated after 16-144 h, depending on when an appropriate amount of CO_2 had accumulated in the Mason jars (depending on the soil layer, the incubation temperature and the progression of incubation).

1.4.5 Data analysis

The mass of CO_2 emitted from each microcosm was calculated according to Paré et al. (2006) and expressed as µg (C) per g of initial carbon mass per day. Cumulative amounts of C mineralized were calculated by adding the cumulative amount of the preceding period with the product of the average of daily mineralization rates of both periods by the number of days between both periods (Maillard et al. 2010).

A first-order kinetic one-compartment exponential model was used to describe the cumulative C mineralization as a function of time:

$$C_{cum}(t) = C_0 * 1\text{-}e^{-k0t},$$

where $C_{cum}(t)$ is the mean cumulative C mineralized at time t (mg C g^{-1} initial C), C_0 the active C or PMC (mg C g^{-1} initial C), k_0 is the decomposition rate constant for mineralization of C (day^{-1}) and t is time (day). We used this model because it is more flexible than more complex models and is widely used to determine active C values. We fitted the C mineralization data of each individual soil sample to the model by means of a least square fitter (SigmaPlot v.10.0, SYSTAT Software, Inc.) and calculated the proportion of PMC at 29°C for each replicated sample.

In order to evaluate the proportion of rapidly-released C (termed "fast C"), indicative of a high-quality organic matter (fast turnover), we used the value of the cumulative C mineralization after 3 months (100 d) of incubation at 29°C. Further characterization of the SOC pool (organic layer only) was done by estimating the size of the stable and the slow C pools by subtracting the value of total C from that of PMC and by subtracting the value of PMC from that of fast C, respectively.

Temperature sensitivity of organic matter decomposition (Q_{10}) was calculated based on equal amounts of C mineralized because previous studies pointed out that Q_{10}s based on C mineralized at the same time may underestimate the temperature responses (Rey and Jarvis 2006; Conant et al. 2008). Hence, we compared the time needed to reach a given amount of C mineralized for each individual microcosm. The microcosm with the lowest cumulative C mineralization set the limit for comparison between stand types (Wetterstedt et al. 2010). Given that the maximum amount of C respired at 2°C represented less than 20 mg of initial C, all the Q_{10}s calculated here belonged to the fast C pool. For that reason, it was not possible to compare Q_{10}s from recalcitrant C with that from fast-labile C materials, as some authors did (e.g. Conant et al. 2008; Xu et al. 2010). Q_{10} values were calculated based on the following equation:

$$Q_{10} = (t_c/t_w)^{10/(T_w - T_c)}$$

where T_c and T_w represent the colder (2 or 14°C) and the warmer (14 or 29°C) temperature, respectively, and t is the time required to respire a given amount of C at a particular temperature.

1.4.6 Statistical analysis

Mean values (e.g. fast C, PMC, total C) were compared between stand types and soil layers using mixed linear models (PROC MIXED). Stand type and soil layer depth were considered as fixed effects whereas replication was considered as a random effect. To meet the assumptions of normality and homoscedasticity, the data were either log10-transformed or square root-transformed. Differences between means were tested using orthogonal contrasts (CONTRAST statement). For presentation of our results, means and confidence limits were converted back to the original scale by reversing the transformation. The significance of the relationship between Q_{10} and C quality was assessed by regression analyses (PROC REG). The significant threshold was set at 0.05, but a significant difference at the 0.10 level was also considered given the inherent large variability in forest soils. Statistical analyses were performed using SAS v. 9.2 (SAS Institute, Cary, NC).

1.5 Results

1.5.1 Amounts and distribution of SOC

For both study regions, SOC stocks of the whole soil profile were not significantly different among stand types (Figure 1.1). However, when considering the different soil layers separately, SOC stocks differed among soil depth and between stand types (Figure 1.1). In both regions, SOC contents decreased from the upper to the lower soil layers. In the ON region, C content of the organic layer was higher in the mixedwood followed by the jack pine and the aspen stands (Figure 1A). In the surface (0-15 cm) and intermediate (15-35 cm) mineral layers, C contents were the highest in aspen stands while no differences were detected in the deepest (35-55 cm) mineral layer. In the QC region, C contents of the organic layer and surface mineral layer were higher in black spruce stands followed by mixedwood and aspen whereas no differences were detected in lower mineral layers (Figure 1.1B).

1.5.2 SOC quality

In both study regions, proportions of fast C and PMC varied significantly with stand type and soil layer depth (Figures 1.2 and 1.3). In the ON region, we observed a gradual decrease in fast C and PMC proportions with depth. In the organic layer, less PMC (9-13% less) was found in stands containing aspen (single- and mixed-species) than under pine. In the deepest mineral layer (35-55 cm), less fast C was found in both single-species stands (pine and aspen) than in mixed-species stands. In the QC region, we observed a more dramatic decrease in fast C and PMC proportion with depth compared with the ON region, and especially at the organic-mineral interface (Figures 1.2 and 1.3). Both spruce and aspen organic layer contained less PMC (6% less) than that of mixed-species stands. Less fast C was found in the organic and surface mineral layers (0-15 cm) of spruce than in that of aspen or mixedwood stands.

Similar to proportions, contents of fast C and PMC varied significantly with stand type and soil layer depth (Figure 1.4). In both regions, fast C and PMC contents decreased from the upper to the lower soil layers. In the ON region, the highest amounts of fast C and PMC were found in the organic layer of mixedwood while the smallest were found for aspen sites (Figures 1.4A and 1.5A). Amounts of stable C in this layer were similar among stand

types but amounts of slow C (PMC fraction) were lower in aspen stands (Figure 1.5A). More fast C was found in the deepest mineral layer in mixedwood than in aspen stands. In the QC region, lowest amounts of fast C, slow C, PMC and stable C were found in the organic layer under aspen (Figures 1.4B and 1.5B). Finally, for all soil layers combined, mixed-species stands of both study regions contained higher amounts of fast C compared with single-species coniferous stands (black spruce and jack pine) (Figure 1.4).

1.5.3 Temperature sensitivity

Cumulative C mineralization was greater at warmer incubation temperatures for all soil samples over the entire duration of the experiment (Figure 1.6). Cumulative C mineralization over the course of the incubation was an average of 2.8 times greater for soils incubated at 14°C compared with 2°C and 2.3 times greater at 29°C compared with 14°C.

In each study region, Q_{10} values were different according to soil layer depth, temperature range and stand type (Table 1.2). On average, Q_{10} values were 1.6 fold higher for the colder temperature range (2-14°C) than for the warmer one (14-29°C). In general, Q_{10} values decreased with increasing depth when expressed using the colder range of temperatures while they were fairly constant when based on the warmer temperature range. In the ON region, Q_{10} values were generally greater in the organic layer of aspen and in mineral layers of stands containing jack pine (single- and mixed-species stands) for the colder range of temperatures (Table 1.2). In the QC region, Q_{10} values were greater in the organic layer of black spruce and in mineral layers of spruce-aspen mixtures for the colder temperature range (Table 1.2).

By comparing SOC quality (determined by the proportion of fast C) with Q_{10} data, we found two contrasting relationships depending on what temperature range was used to calculate Q_{10} values (Figure 1.7). For the colder temperature range, Q_{10} increased drastically (i.e. from 1-4) for SOC of the lowest to the highest quality found in the mineral layers (i.e. from 15-40 mg fast C g^{-1} total C) and then more gradually in the organic layer. When based on the warmer temperature range, Q_{10} decreased with increasing C quality in mineral layers and then increased with C quality in the organic layer. When calculating Q_{10} values for the

entire range of temperatures (2-29°C), the relationship between Q_{10} and SOC quality was not significant (data not shown).

1.6 Discussion

As with parent material, time, topography and climate, the biota belongs to the five factors of soil formation according to Hans Jenny's classic concept (1994). Expectedly, several studies have shown an influence of tree species composition on soil properties (e.g. pH, C and nutrient contents, soil community composition) and soil ecological processes (e.g. decomposition, nutrient mineralization) (e.g. Binkley 1995; Wardle et al. 1997; Laganière et al. 2009). However, species-related differences have been mainly observed for the organic layer (Wardle et al. 1997; Alriksson and Eriksson 1998; Reich et al. 2005; Hobbie et al. 2006; Laganière et al. 2009, 2010b) and most rarely in the mineral layer (Finzi et al. 1998; Giardina et al. 2001; Vesterdal et al. 2008). In our study, we detected a significant difference (for fast C, PMC or total C) between stand types not only in the organic layer, but also in the surface mineral layer (0-15 cm) of both study regions and for the intermediate (15-35 cm) and deep (35-55 cm) mineral layers of the ON region.

While SOC stocks of the whole soil profile were not significantly different among stand types, probably owing to high variability and low sampling effort in deep horizons, the distribution of C across layers of the soil profile varied with forest composition. In the ON region, the greatest organic layer C stocks were found in mixed-species while the lowest were found in aspen stands. The inverse was true for the entire mineral layer C stocks but a higher concentration of silt particles in aspen stands (data not shown) may be in part responsible for this greater C accumulation observed for this stand type in the ON region because fine mineral particles increase organic matter stabilization (von Lützow et al. 2006). In the QC region, the greatest amount of surface SOC (organic + surface mineral layer) was found in black spruce stands while the lowest stock was also found in aspen stands and mixed stands were intermediate. SOC stocks below 15 cm were similar across stand types. Hence, the tendency for species favouring low soil C contents near the surface to have more C in deeper soil layers, as highlighted by Vesterdal et al. (2008), was only partly supported by our observations.

1.6.1 Organic layer SOC

Stands containing coniferous species (single- and mixed-species) stored greater amounts of organic layer SOC than single-species aspen stands (Figure 1.1). The surface accumulation of SOC is mainly driven by rates of C input (litterfall) and by C protection mechanisms such as the biochemical quality of litter and environmental constraints that affect rates of decomposition (Jandl et al. 2007). Although annual tree litterfall under broadleaved species may be greater than under conifers, the needle litter from conifers is often acidic, molecular-complex and generally less palatable for soil decomposers compared with broadleaves (Aerts and Chapin 1999; Wardle 2002). In addition, the understory vegetation associated with coniferous stands (i.e. bryophyte) is a major source of surface SOC and may surpass by several times the amount of tree-originated C returned to the soil (Oechel and Van Cleve 1986). Bryophytes also favour cold and wet field conditions and, in general, they decompose slowly (Légaré et al. 2005b; Gornall et al. 2007; Lang et al. 2009). The latter affirmation was corroborated by the observed lowest proportion of fast C found in the organic layer of black spruce, indicating a slow C turnover even under optimal laboratory conditions (Figure 1.3B). Therefore, accumulation of surface SOC would be favoured in conifer stands because C output rates are generally limited by micro-environmental conditions and by the nature of C inputs that decompose slowly.

In the ON region, however, the greatest amount of C found in the organic layer was in mixedwoods and not in pure coniferous stands, i.e. jack pine (Figure 1.1A). Similarly, in the same area, Brassard et al. (2011) found mixed-species stands to have higher fine root productivity and spatial distribution while Cavard et al. (2010) found no relationship between tree diversity and aboveground tree productivity. Greater C accumulation in the organic layer thus correlates with the belowground component but not with the aboveground one. Different mechanisms have been suggested that could make mixed-species stands more efficient than single-species ones in having a greater biomass accumulation: facilitation, niche partitioning and greater stability (resistance) to disturbances (Jandl et al. 2007; Lorenz and Lal 2010). Along with a low proportion of PMC (Figure 1.3A), the possible occurrence of these mechanisms may explain the synergistic response of organic layer SOC storage to the aspen-jack pine mixture.

A large part of the C found in the organic layer of both regions was active SOC. The size of the PMC pool ranged from 16% to as high as 49% of SOC, with an average ± standard deviation of 27 ± 8% (data not shown). Likewise, Neff and Hooper (2002) estimated that soils of northern latitudes may contain around 9-41% of potentially mineralizable C. Although nearly three quarters of organic layer SOC may be qualified as stable in our study (Figure 1.5), the active SOC pool of the boreal biome is considerable in absolute numbers and is still substantially greater than that found in other biomes (temperate and tropical), where the active pool generally represents only 2-3% and is far less important on an absolute basis (Neff and Hooper 2002; Fissore et al. 2009). Accordingly, as pointed out by Neff and Hooper (2002), the response of decomposition to warming could be less constrained by C availability in boreal than in temperate or tropical soils. Furthermore, since the proportions of active C varied among stand types (Figure 1.3), the overall stability of organic layer SOC stocks differed with forest composition in the boreal biome. Given that less PMC (active C) was generally found in aspen stands, the organic layer SOC of aspen may be considered more stable (Figure 1.3).

In terms of thermal sensitivity to decomposition, higher Q_{10}s were found in the organic than in the mineral layers when the colder temperature range was considered (Table 1.2). Similar results were also reported by a number of studies (e.g. Paré et al. 2006; Jonard et al. 2007). Hence, the impact of global warming may be more pronounced in stand types storing the largest amount of active SOC in their organic layer such as in stands containing conifers (single- and mixed-species) and especially in stands containing black spruce (Figure 4). Our results also suggest that the usual Q_{10} of 2 used in coupled climate-carbon cycle models seems inappropriate for microbial decomposition occurring in northern soils where soil temperatures below 15°C prevail.

1.6.2 Mineral layer SOC

Accumulation of SOC in mineral layers is more complex. It depends on both aboveground and belowground C sources (e.g. dissolved organic C from the organic layer, root litterfall and rhizodeposition) and involves important stabilization mechanisms including chemical and physical protection within soil aggregates (Rumpel and Kögel-Knabner 2011).

Probably in response to these differences in C sources and in protective capacity of SOC, we found a decrease in cumulative C mineralization and in fast C and PMC proportions from the organic to the mineral layers and this decrease was more pronounced in the clayey soils of the QC region than in the sandy soils of the ON region (Figures 1.2 and 1.3). This divergence between both regions is not surprising since fine mineral particles (i.e. silt and clay) protect SOC against microbial use via the formation of organo-mineral complexes (von Lützow et al. 2006).

In a previous experiment aiming to evaluate the influence of forest composition on soil aggregation and soil size-density fractions in the surface mineral layer of the QC sites, Laganière et al. (2011; Chapter II) showed that contents of the less protected fractions (i.e. uncomplexed organic matter), commonly considered as the active pool of SOC, corresponded to 16.0, 11.3 and 7.7 Mg C ha^{-1} under black spruce, mixedwood and aspen stands, respectively. In comparison, we found a similar (but not significant) decreasing trend in PMC contents among stand types but the estimation of our biologically active SOC pools was lower (3.8, 3.7 and 3.4 Mg C ha^{-1}, respectively; Figure 1.4B). This might be explained because uncomplexed organic matter may contain not only active SOC but also biochemically resistant SOC and a variable proportion of particulate organic matter physically protected within macroaggregates that is not readily available for microbes (Gregorich et al. 2006; von Lützow et al. 2007).

Across the soil profile, SOC located in deep layers would be more stable than surface SOC for several reasons including the fact that low temperature and heterogeneity of C input in depth limit microbial activity (Salomé et al. 2010; Rumpel and Kögel-Knabner 2011), because deep SOC is protected against combustion during wildfire (Neff et al. 2005) and because deep SOC decomposes more slowly than surface SOC, as shown by lower proportions of fast C below 15 cm depth (Figure 1.3). In general, deep-rooting tree species tend to accumulate more C in deep soil layers while species with a shallow root system tend to accumulate C in the upper layers (Lorenz and Lal 2010). Our results are in line with this affirmation. While the root system of aspen and jack pine can reach a depth of 100 cm, black spruce roots rarely exceed 30 cm and most of the root system is located at the organic-mineral interface (Strong and La Roi 1983). These specific root patterns apparently coincide

with SOC accumulation patterns of our study sites. Only 25% of the total SOC stock under black spruce was located below 15 cm depth compared with 36% for jack pine, and with 36% and 46% for trembling aspen in the QC and the ON region, respectively (30% for both mixedwoods) (Figure 1.1). When correcting for the higher silt concentration in aspen stands of the ON region by setting silt as a covariable (mineral soil from aspen had an average of 18% greater silt concentration than that from jack pine and mixedwood), the highest contribution of deep SOC was still found in aspen stands with 41% of the total SOC stock (data not shown). Consequently, on the basis of C distribution across the soil profile, the SOC stock under trembling aspen could be qualified as more stable because a larger part of SOC is distributed in deep soil layers, where organic matter quality is lower and conditions for microbial activity are harsher relative to the other stand types.

1.6.3 Temperature sensitivity vs. SOC quality

According to enzyme kinetics, the more biochemically recalcitrant the organic matter, the greater the temperature sensitivity of microbial decomposition (Davidson and Janssens 2006). Despite this simple thermodynamic law, the temperature sensitivity vs. SOC quality hypothesis is still debated among the scientific community. Some of the past research has supported relationships that follow this hypothesis (Fierer et al. 2005; Conant et al. 2008; Craine et al. 2010) and some did not (Liski et al. 1999; Fang et al. 2005; Reichstein et al. 2005; Fissore et al. 2009). By using various published data, Conant et al. (2008) and, more recently, Craine et al. (2010) provided further evidence that Q_{10} increased with decreasing SOC quality. The same relationship was found in our study for the mineral soil samples when Q_{10} values were based on a relatively similar range of temperature (this study: 14-29°C; Conant et al. 2008 and Craine et al. 2010: 20-30°C). However, when Q_{10} values were based on a range of temperatures that is more commonly experienced by boreal soils (i.e. 2-14°C), the opposite relationship was observed. The apparent temperature sensitivity of mineral SOC decomposition increased with SOC quality.

Using a single, wide range of temperature (4-44°C) to calculate Q_{10} values, Fang et al. (2005) found no significant relationship between Q_{10} and SOC quality, in line with our observations, when the entire range of temperatures was used (2-29°C). This may result from calculating a unique Q_{10} for the entire range of temperatures, as underscored by Karhu et al.

(2010), and further from the subtraction of the positive linear relationship between Q_{10} and SOC quality at low temperatures with the inverse linear relationship at warmer temperatures, as observed in our study.

Further investigations are required to determine why the slope of the relationship between Q_{10} and SOC quality varies with temperature. It might be the result of a change in the soil microbial community among temperature ranges such that a particular range of temperatures would favour the establishment of a particular community that has a different substrate quality use upon warming. However, measuring a constant Q_{10} calculated as an average over the whole temperature range proved to mask the influence of temperature on Q_{10} values and could explain some of the contradictory results from earlier studies (Karhu et al. 2010). Our results highlight the importance of calculating Q_{10} values based on a temperature range that closely represents field temperature rather than on the range commonly used (i.e. 20-30°C), especially when aiming to evaluate northern ecosystem feedback related to climate change.

1.7 Conclusion

We showed that distribution and quality of SOC differed among stand types of the Canadian boreal forest. In general, SOC from aspen was the most stable, as exemplified by larger amounts of deep SOC and a lower proportion of PMC in the organic layer. Low quality C inputs (with low fast C proportions) and soil microclimatic conditions limiting decomposition typically found in black spruce stands however seemed to allow a greater accumulation of SOC in surface layers. Nevertheless, these stocks might become vulnerable to extra SOC losses not only if soil conditions become more favourable to decomposition under climate change, but also because the temperature sensitivity of decomposition was the highest for the study region. We also found that temperature sensitivity of SOC decomposition occurring in the mineral soil increased with the proportion of fast C (i.e. with increasing SOC quality) when the calculations were based on a temperature range commonly experienced in these soils (below 15°C), suggesting that the response of northern soils to global warming could only be transient as it might be controlled by the amount of labile SOC. Collectively, our results highlighted that change in boreal forest composition could have implications for stability of SOC stocks and reaction to climate change.

1.8 Acknowledgements

This study was funded through a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Project Research Grant and the Fonds québécois de la recherche sur la nature et les technologies (FQRNT). We acknowledge the support from Abititi-Bowater, Tembec, BIOCAP Canada, the Ontario Ministry of Natural Resources, and the Canadian Forest Service. We are grateful to Luc St-Antoine, Éric Girard, Jessie Parent, Stephen Hart, and Alain Courcelles for their valuable assistance in the field and in the laboratory. We thank Michèle Bernier-Cardou for her statistical assistance and Yan Boulanger for comments on an earlier version of the manuscript.

Table 1.1 Tree species composition (mean % tree basal area ± SE) of the stand types located in two study regions of the Canadian boreal biome (ON region, n=5; QC region, n=8).

Tree species	ON region			QC region		
	Jack pine	Mixedwood	Aspen	Black spruce	Mixedwood	Aspen
Trembling aspen	1.6 ± 1.5	35.5 ± 6.75	95.5 ± 1.11	1.5 ± 0.6	61.4 ± 4.1	88.9 ± 2.2
Jack pine	83.3 ± 3.00	53.7 ± 7.09	0.7 ± 0.7	-	-	-
Black spruce	-	-	-	91.1 ± 3.4	33.5 ± 3.9	8.9 ± 1.7
Other species[1]	15.2 ± 2.13	10.8 ± 1.69	3.9 ± 0.8	7.4 ± 3.1	5.1 ± 1.5	2.2 ± 2.0

[1]Other species include jack pine and balsam fir (*Abies balsamea* (L.) Mill.) for the QC region and balsam fir, white spruce (*Picea glauca* (Moench) Voss) and white birch (*Betula papyrifera* Marsh.) for the ON region.

Table 1.2 Temperature sensitivity of SOC decomposition (Q_{10}) within layers of the soil profile of different stand types located in two study regions of the Canadian boreal biome (pooled samples).

Range of Temperature	Soil layer[1]	ON region			QC region		
		Jack pine	Mixedwood	Aspen	Black spruce	Mixedwood	Aspen
2-14°C	ORG	4.1	4.4	5.2	4.4	3.3	4.1
	0-15	3.9	3.8	3.7	3.0	4.0	3.3
	15-35	3.7	3.8	3.5	1.9	3.0	2.2
	35-55	2.7	3.5	1.8	1.2	1.9	1.2
14-29°C	ORG	1.9	1.9	2.2	1.9	1.8	1.5
	0-15	2.3	1.8	1.8	2.8	2.8	2.8
	15-35	2.2	1.5	2.0	2.9	1.7	2.7
	35-55	2.0	1.7	2.8	2.0	2.4	1.7

[1]ORG, organic layer; 0-15, surface mineral layer 0-15 cm; 15-35, intermediate mineral layer 15-35 cm; 35-55, deep mineral layer 35-55 cm.

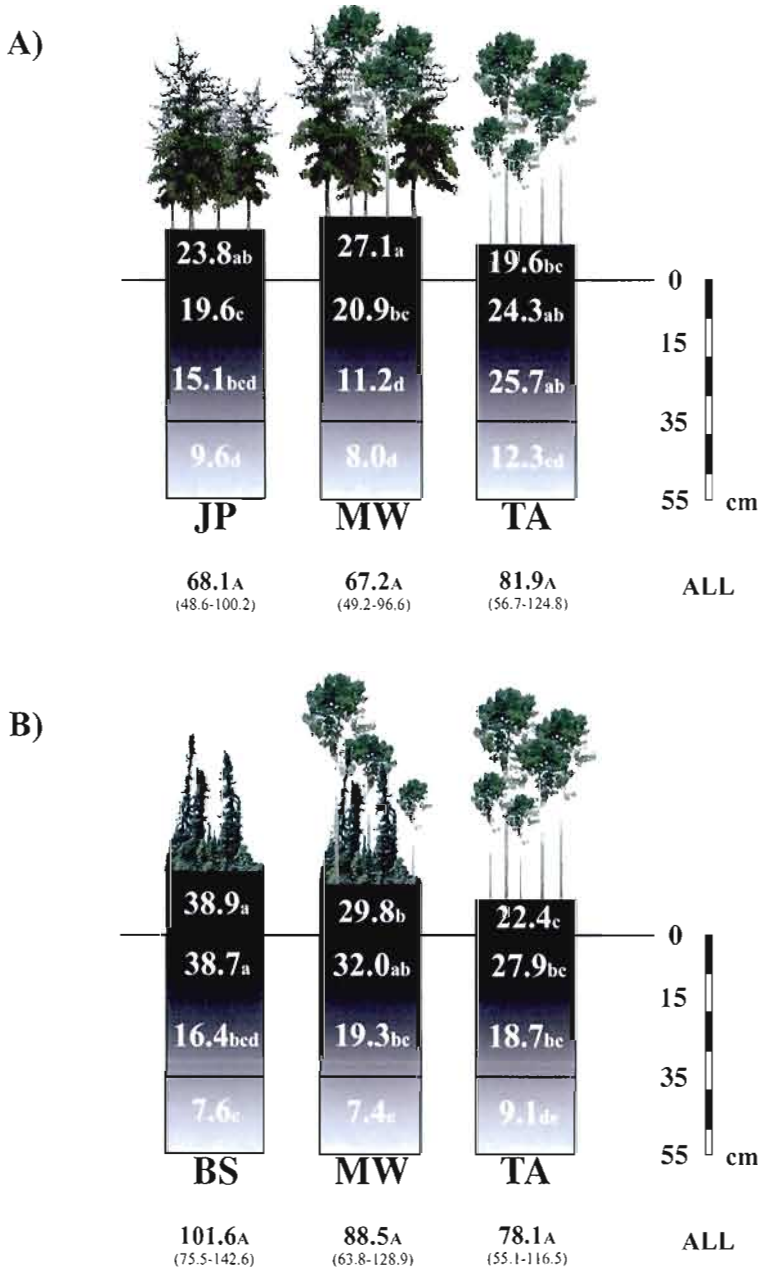

Figure 1.1 Amounts and distribution of SOC stocks in different stand types located in the ON (A) and in the QC (B) regions of the Canadian boreal biome. Different letters represent a statistical difference between means according to mixed linear models as described in the Materials and Methods section. 95% confidence limits are shown for the total SOC stocks. BS, black spruce; JP, jack pine; MW, mixedwood; TA, trembling aspen. ON region, n=5; QC region, n=8.

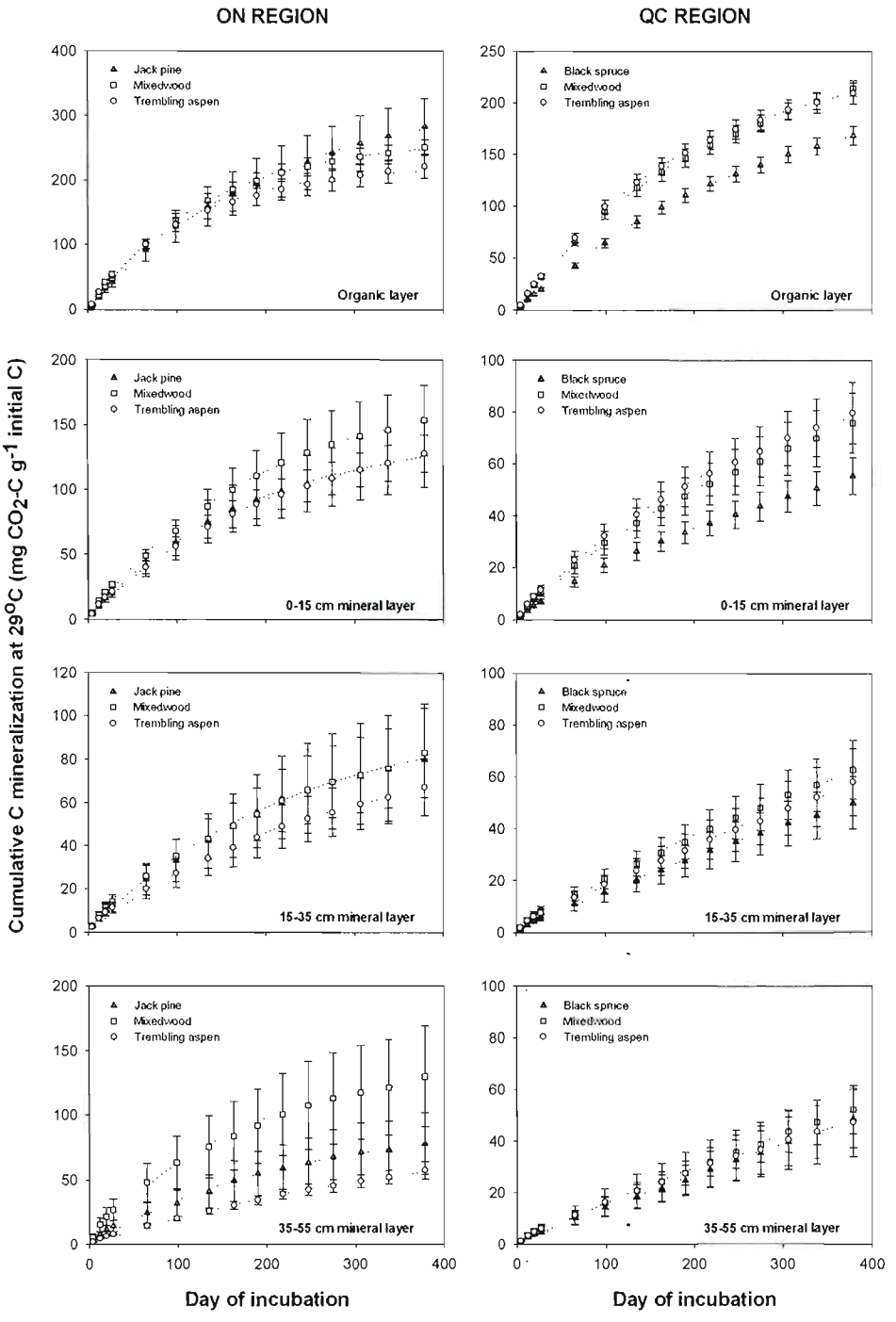

Figure 1.2 Cumulative C mineralized within layers of the soil profile in different stand types located in two regions of the Canadian boreal biome during 379 days of incubation at 29°C. Scale of y-axis is not constant among soil layers and regions. Error bars are ± SE. ON region, n=5; QC region, n=8.

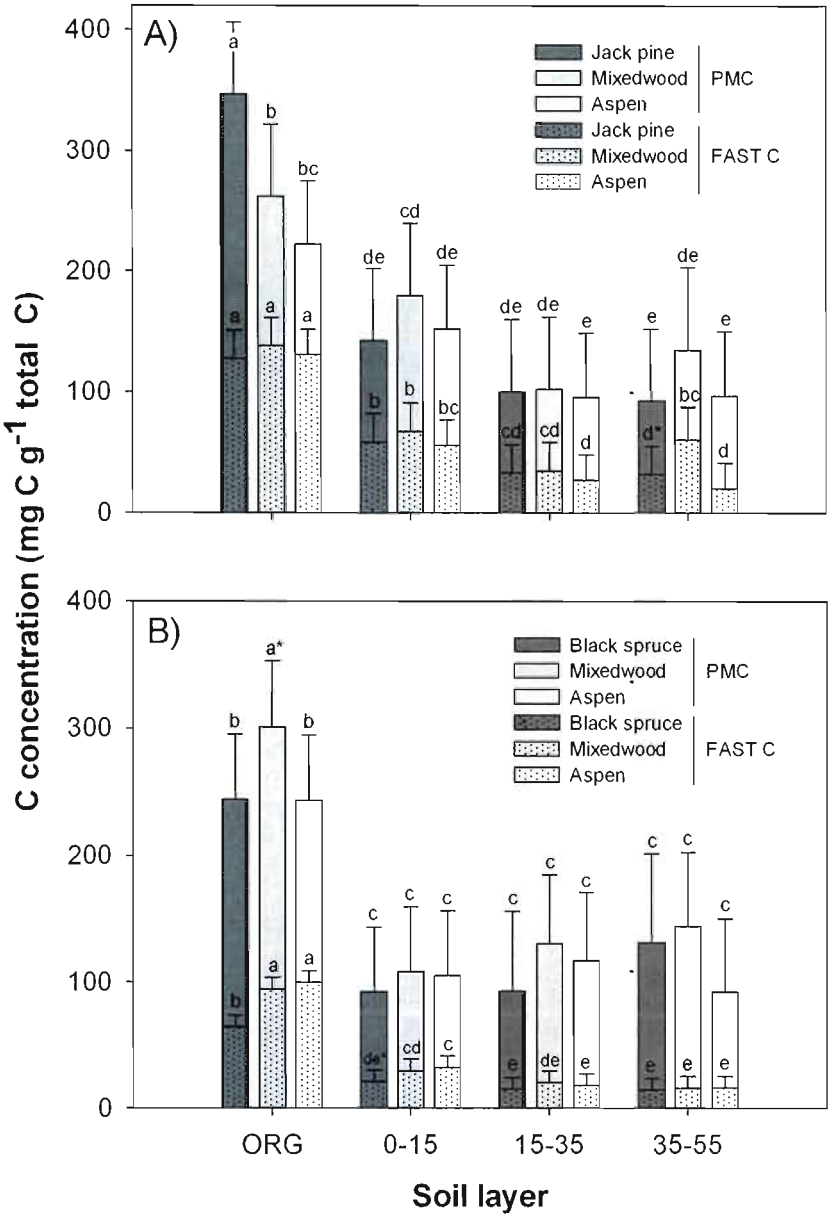

Figure 1.3 Proportions of fast C and PMC (potential mineralizable C) contained in SOC stocks within layers of the soil profile in different stand types located in the ON (A) and in the QC (B) regions of the Canadian boreal biome. Different letters represent a statistical difference between means at $p<0.05$ (or $p<0.10$ when identified with an asterisk) according to mixed linear models as described in the Materials and Methods section. Error bars are 95% upper confidence limits. ON region, n=5; QC region, n=8.

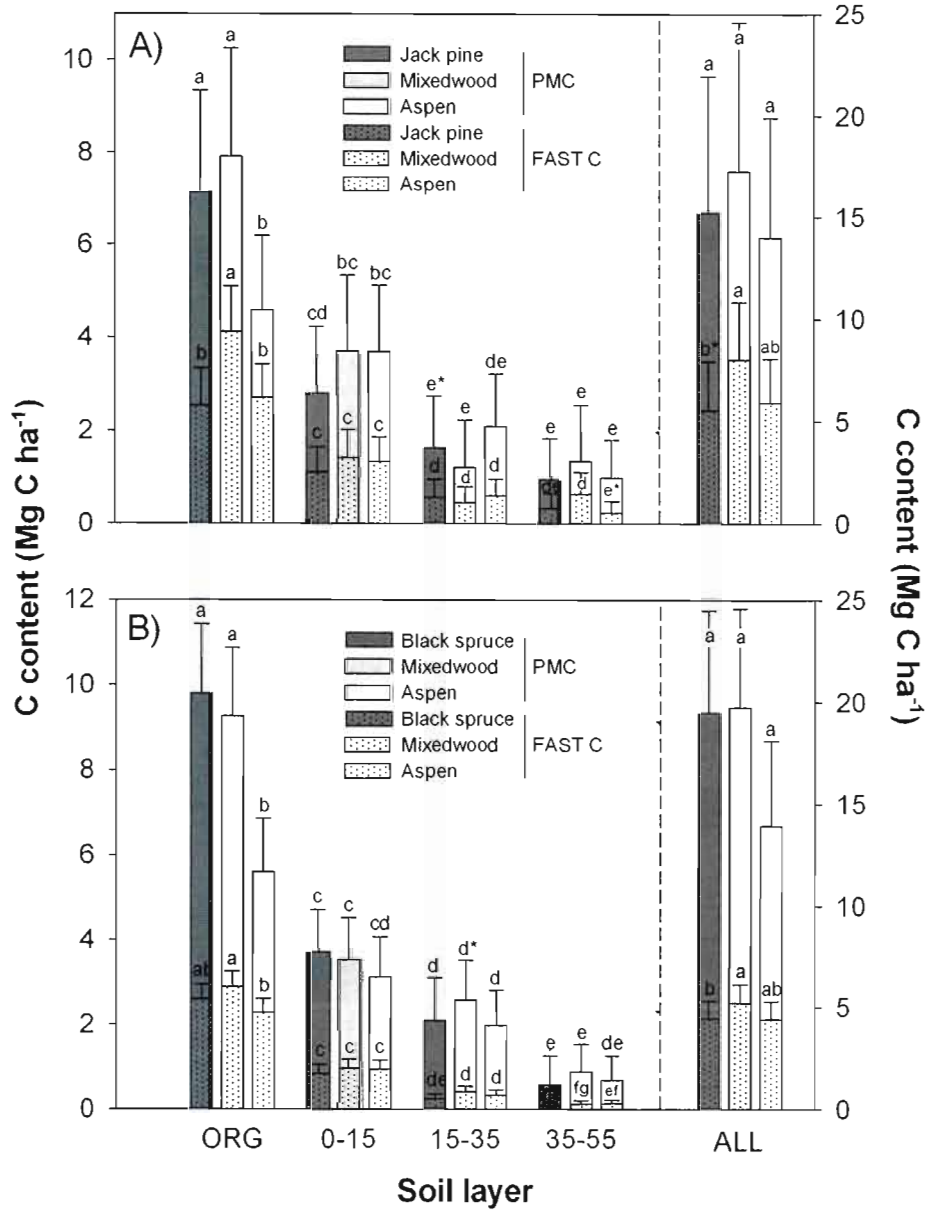

Figure 1.4 Amounts of fast C and PMC (potential mineralizable C) contained within layers of the soil profile in different stand types located in the ON (A) and in the QC (B) regions of the Canadian boreal biome. Scale of y-axis is not constant among regions. Different letters represent a statistical difference between means at $p<0.05$ (or $p<0.10$ when identified with an asterisk) according to mixed linear models as described in the Materials and Methods section. Error bars are 95% upper confidence limits. ON region, n=5; QC region, n=8.

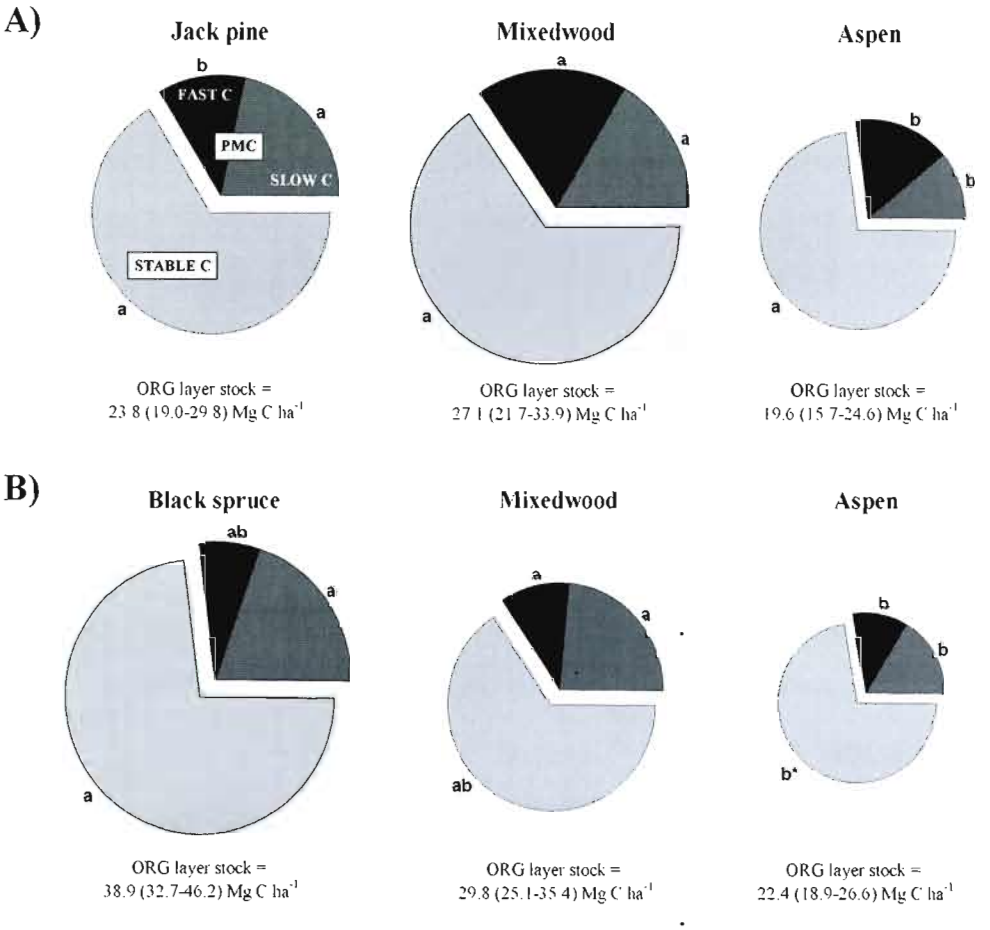

Figure 1.5 Contribution of different C fractions (fast C, slow C and stable C) to total organic layer (ORG) SOC stock in different stand types located in the ON (A) and in the QC (B) regions of the Canadian boreal biome. The size of pie charts is proportional to total SOC stocks for a given region. Different letters represent a statistical difference between means at $p<0.05$ (or $p<0.10$ when identified with an asterisk) according to mixed linear models as described in the Materials and Methods section. ON region, n=5; QC region, n=8.

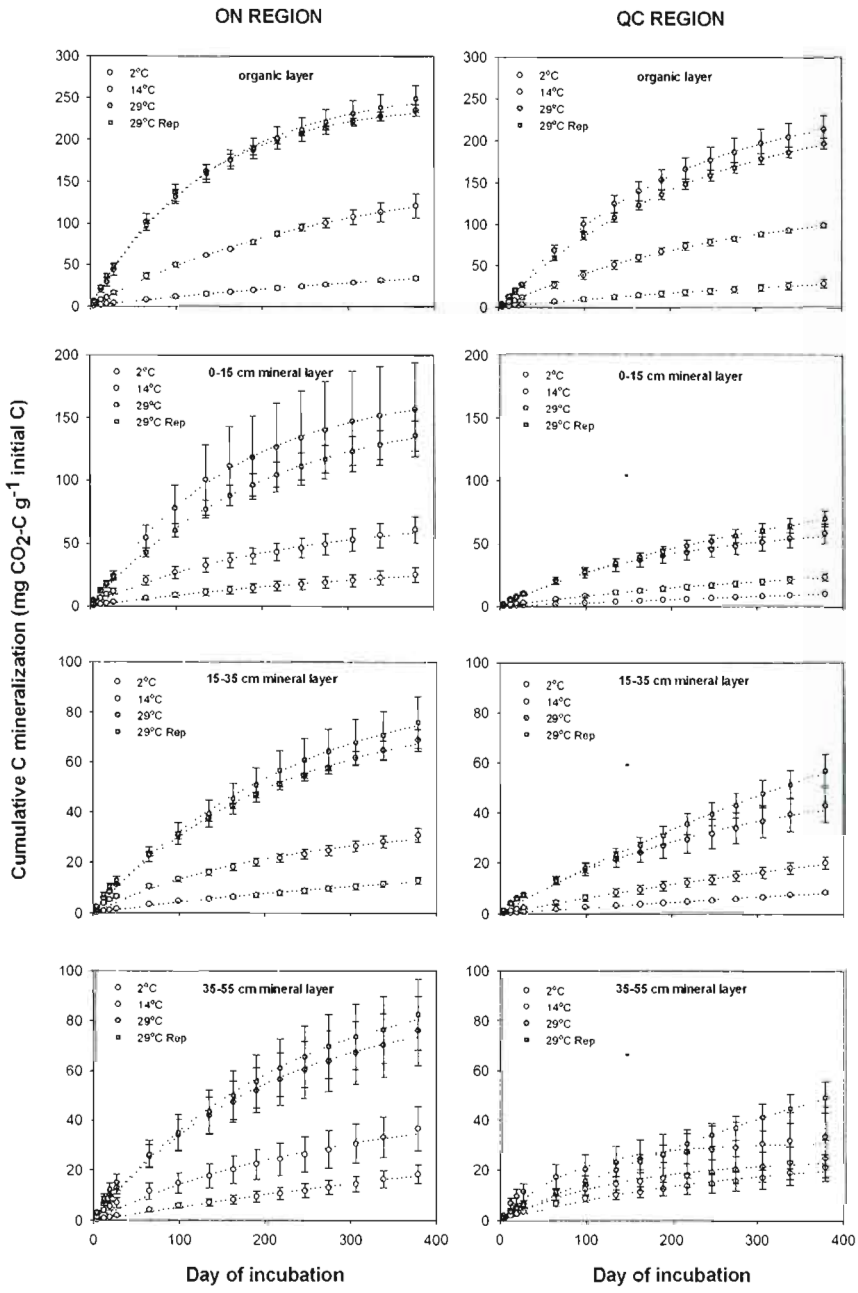

Figure 1.6 Cumulative C mineralized within layers of the soil profile located in two regions of the Canadian boreal biome during 379 days of incubation at 2, 14 and 29°C. Scale of y-axis is not constant among soil layers. Error bars are ± SE. Replicated mineralization curves at 29°C (29°C Rep) are shown to confirm the similarity of response between pooled (QC and ON regions, n=3) and non-pooled soil samples (ON region, n=15; QC region, n=24) at 29°C.

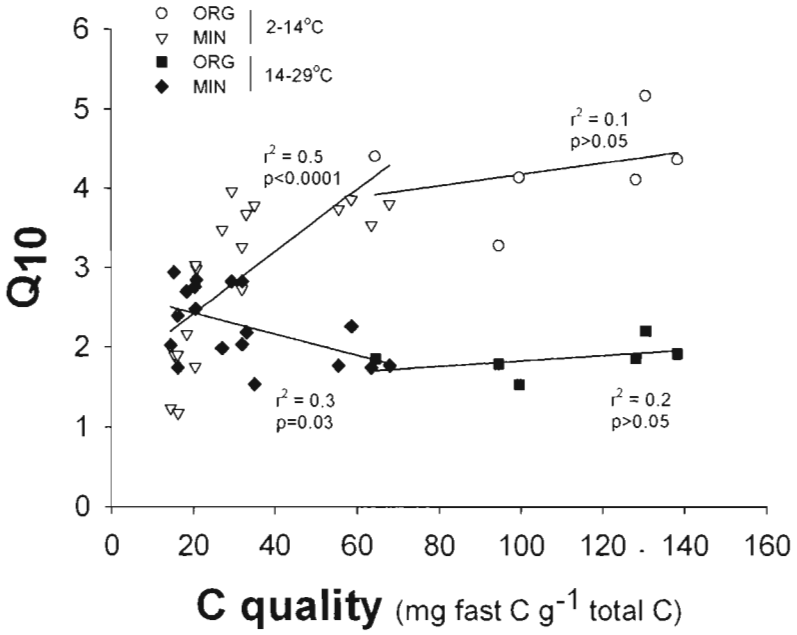

Figure 1.7 Relationship between Q_{10} and C quality for the colder (2-14°C) and the warmer (14-29°C) temperature ranges. Each dot represents the Q_{10} of one pooled sample linked to its C quality estimated as the proportion of total C lost after 100 days of incubation at 29°C. ORG, organic layer; MIN, mineral layer.

CHAPITRE II

BLACK SPRUCE SOILS ACCUMULATE MORE UNCOMPLEXED ORGANIC MATTER THAN ASPEN SOILS

Dans le chapitre précédent, j'ai estimé les stocks de COS pour différents types de peuplements. J'ai montré que la stabilité du COS variait avec la composition forestière à cause de variations dans la distribution verticale, dans la qualité et dans la réponse du COS à l'augmentation de la température (stabilité thermique). Dans ce deuxième chapitre, j'essayerai d'établir que la composition forestière influence la répartition du C dans les fractions physiques du sol, qui est une méthode complémentaire à celles utilisées dans le premier chapitre pour estimer la stabilité du C contenu dans le sol minéral. Ce travail est original par le fait que l'effet de la composition forestière sur les agrégats de sol et fractions physiques a rarement été démontré expérimentalement et spécialement dans les sols forestiers en conditions naturelles.

Tous les co-auteurs ont contribué à la conceptualisation et à l'élaboration du design expérimental de l'étude et à la révision du présent article scientifique. JL a exécuté la recherche, analysé les données et écrit l'article. Les analyses de fractionnement ont été réalisées dans les laboratoires de DAA. HYHC est le chercheur principal du projet stratégique CRSNG dans lequel mon doctorat s'est inscrit. La référence de l'article est :

Laganière, J., D.A. Angers, D. Paré, Y. Bergeron et H.Y.H. Chen. 2011. Black spruce soils accumulate more uncomplexed organic matter than aspen soils. Soil Science Society of America Journal, 75: 1125-1132.

2.1 Résumé

Accroître les connaissances sur la dynamique du réservoir de carbone du sol de la forêt boréale revêt une importance particulière en réponse à des préoccupations environnementales comme les changements climatiques. Nous avons émis l'hypothèse que différents types de peuplements (pessière noire, tremblaie et forêt mixte) développés sur des sites similaires affecteraient la distribution du carbone organique du sol (COS) dans les fractions physiques du sol. Le sol minéral de surface (0-15 cm) de 24 parcelles de composition forestière différente a été échantillonné dans des Luvisols forestiers de l'Abitibi-Témiscamingue et de la Baie-James, Canada. Le sol a premièrement été séparé en trois fractions d'agrégats stables à l'eau de tailles différentes (>1000 µm, 1000-250 µm et <250 µm) par tamisage humide, suivi d'une séparation par densité (NaI: 1,7 g cm^{-3}) et d'une dispersion (avec des billes de verre) pour isoler la fraction légère (FL), la matière organique particulaire intra-agrégat (iMOP) et la fraction limon-argile (L&A). D'après des modèles linéaires mixtes, les contenus en COS du sol entier (en Mg C·ha^{-1}) diminuaient dans l'ordre suivant: pessière noire (46,3)>forêt mixte (41,9)>tremblaie (34,7). Bien que des contenus comparables en COS (~30 Mg C ha^{-1}) ont été trouvés dans la fraction L&A, plus de COS a été trouvé dans les fractions les moins protégées (c.-à-d. dans la matière organique non associée aux particules minérales : FL et iMOP) dans les pessières noires que dans les tremblaies, les forêts mixtes ayant des valeurs intermédiaires. Cette plus grande accumulation de matière organique non associée aux particules minérales dans les pessières noires suggère un taux de renouvellement du C plus lent qui est probablement dû à des apports de C de faible qualité et à des contraintes environnementales à la décomposition généralement retrouvées dans ce type de peuplement. Ces différences de contenus de COS stockés dans les différentes fractions physiques du sol pourraient avoir de grandes répercussions sur le bilan de COS de la forêt boréale canadienne sous l'effet des changements climatiques.

2.2 Abstract

Improving knowledge on the dynamics and maintenance of the boreal soil's C pool is of particular importance in response to climate change concerns. We hypothesized that different forest types (black spruce, trembling aspen and mixedwood) found on a similar site type differentially affect soil organic C (SOC) distribution among physical fractions. The surface mineral soil (0-15 cm) of 24 plots differing in forest composition was sampled in forested Luvisols of the Abitibi-James Bay region, Canada. The soil was first separated into three water-stable aggregate size fractions (>1000 μm, 1000-250 μm and <250 μm) by wet sieving, followed by a density flotation (NaI: 1.7 g cm^{-3}) and a dispersion (with glass beads) to isolate the free light fraction (LF), the intra-aggregate particulate organic matter (iPOM) and the silt plus clay fraction (S&C). According to mixed linear models, whole SOC contents (in Mg C ha^{-1}) decreased in the following order: black spruce (46.3)>mixedwood (41.9)>trembling aspen (34.7). While similar amounts of SOC (~30 Mg C ha^{-1}) were found in the S&C, more SOC was found in the less protected fractions (i.e., uncomplexed organic matter, UOM: LF and iPOM) under black spruce than under trembling aspen, the mixedwood being intermediate. This higher accumulation of UOM under black spruce suggests a slower C turnover that is probably induced by the low-quality C inputs and environmental constraints to decomposition found in these forests. These differences in the amounts of SOC stored within soil physical fractions might have strong repercussions on the SOC budget of the boreal forest of eastern Canada under climate change.

2.3 Introduction

Boreal soils hold one of the largest pools of terrestrial carbon in the form of soil organic carbon (SOC), storing around three times more SOC than temperate or tropical biomes (Lal 2005). Accordingly, any variation in the size and turnover rate of this major C pool could alter atmospheric CO_2 concentration and global climate.

The residence time of C in soils is highly variable, ranging from a few days to thousands of years (von Lützow et al. 2006). SOC stabilization and accumulation depend on a variety of factors, including C input rate and quality, and soil microclimatic conditions such as temperature and moisture that greatly affect the C output rate, i.e., decomposition (Lorenz and Lal 2010). Stabilization of SOC also occurs when organic matter and mineral particles are mixed together to form organo-mineral complexes. Tisdall and Oades (1982) conceptualized a hierarchical structure for soil aggregation that involves a distribution of organic matter into differently sized aggregates with varying degrees of stability. Interactions between organic matter, roots, microbes and mineral particles generate macro-aggregates (>250 μm) that contain C in various soil fractions, namely microbial biomass, free organic matter (e.g., light fraction or LF), intra-aggregate particulate organic matter (iPOM), and the silt plus clay fraction (S&C) (Figure 2.1). While the former fractions are generally considered to be relatively labile, C in iPOM would be physically protected from microbial degradation by occlusion within aggregates whereas C associated with S&C would be further protected by chemical association with mineral surfaces (Blanco-Canqui and Lal 2004; von Lützow et al. 2006). As macro-aggregates become older, they disrupt into several, more stable fractions called micro-aggregates (<250 μm) (Angers et al. 1997), which may recombine into macro-aggregates thereafter (Six et al. 2000).

The formation and stabilization of aggregates depend on abiotic factors such as soil mineralogy, texture, cation content and sesquioxides content (aluminum and iron oxides), as well as biotic factors such as organic matter quantity and quality, diversity and abundance of soil organisms, and especially the presence of macrofauna (Bossuyt et al. 2006; Abiven et al. 2009). Most of these variables are singularly affected by the nature of the forest cover, i.e., tree species composition (Flanagan and Van Cleve 1983; Binkley and Valentine 1991;

Hodson and Sangster 1999; Hobbie et al. 2006; Laganière et al. 2009). Hence, the stability of SOC stocks should vary according to tree species composition.

In the Canadian boreal forest, black spruce (*Picea mariana* [Mill.] BSP) is the most common tree species, covering more than 150 million ha (Canada's NFI 2010). Black spruce forests accumulate large quantities of SOC in their forest floor and surface mineral layers in response to both poor litter quality (i.e., biochemical recalcitrance) and the cold and wet microclimatic conditions associated with this forest type that limit the activity of soil decomposers (Fenton et al. 2005; Lavoie et al. 2005; Laganière et al. 2009). Over the past century, we have observed an expansion of broadleaved tree species such as trembling aspen (*Populus tremuloides* Michx.) over a large area of the boreal forest that is probably induced by a change in the frequency of human and/or natural disturbances such as road construction, forest cutting activities, wildfire and insect outbreaks (Ilisson and Chen 2009a; Laquerre et al. 2009). The presence of aspen patches within black spruce-dominated forests has been related to better litter quality and enhancement of soil microclimatic conditions, resulting in attendant increases in soil biological activity and decomposition rates (Légaré et al. 2005b; Laganière et al. 2009, 2010b). Consequently, an increase in the relative abundance of aspen at the landscape level may have implications in terms of SOC storage and stability. While the effect of black spruce and aspen on C stabilization through litter quality and soil microclimate is well understood, how these two tree species affect C stabilization through soil aggregation and soil physical fractions is unknown. Improving knowledge on the dynamics and maintenance of such a major C pool is of particular importance in response to climate change concerns and greenhouse gas mitigation efforts (Cole et al. 1996).

The aim of this study was to explore the influence of black spruce and trembling aspen, either in pure stands or in mixtures, on C distribution among soil aggregate size classes and soil physical fractions. The proportions and contents of C associated with LF, iPOM, and S&C were determined in forested Luvisols of the eastern Boreal Shield, Canada. The proportions of C contained within water-stable macro- and micro-aggregates were also determined. We hypothesized that the higher soil biological activity usually found under broadleaved tree species (Laganière et al. 2009) would be reflected by lower SOC content

under aspen than under black spruce but a higher proportion of C protected inside aggregates (i.e., iPOM and S&C).

2.4 Materials and methods

2.4.1 Study area and sampling

The study area is located in the Eastern Boreal Shield of Canada, in the Abitibi-James Bay region of Quebec (49°08'N to 49°11'N, 78°46'W to 78°53'W). This region is part of the black spruce-feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) forest of western Quebec (Grondin 1996). This domain extends over the Clay Belt region of Quebec and Ontario, a major physiographic region resulting from the deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse, in the Wisconsinan glacial age (Vincent and Hardy 1977). A large part of this region is characterized by homogeneous site conditions, i.e., a flat topography, a fine-textured parent material (~50% clay), and Luvisols as the main soil type (Soil Classification Working Group, 1998). The dominant disturbance type is large fires that kill all aboveground vegetation. The climate is boreal with a mean annual temperature of 0.7°C and annual precipitation of 890 mm (Environment Canada 2010).

Eight mature forest sites dominated by black spruce and trembling aspen, each ranging from pure stands to a variety of mixtures of both species, were selected for the purpose of the study (for soil sampling). These sites were located in an area of 36 km^2 with a maximum distance of 7 km between sites. At each site, three 400 m^2 sampling plots were randomly established: one dominated by black spruce, one dominated by aspen, and the third one, mixed uniformly with both tree species. The vegetation under spruce canopy included mainly Labrador tea (*Ledum groenlandicum* Oeder), *Vaccinium* spp., and feathermoss (*Pleurozium schreberi* (Bird.) Mitt.); the latter was the dominant ground cover and an important input of organic matter to the soil (Bisbee et al..2001). The aspen understory included herbs and isolated clumps of speckled alder (*Alnus rugosa* (Du Roi) Spreng.) while the mixedwood understory comprised a mixture of those found under spruce and aspen. The sampling plots were separated by a distance of 40-100 m to minimize variability within a site. All sites originated from the same fire that occurred in 1916 (Légaré et al. 2005a). During the selection of the sites, particular attention was given to ensuring the similarity of permanent

site conditions (Tables 2.1 and 2.2). Thus, any variation in the dependent variables is assumed to be the effect of tree species and their associated understory. More information on stand characteristics is found in Cavard et al. (2010).

In October 2008, four surface mineral soil samples (0-15 cm depth) were carefully extracted from each plot with a metal corer (diam: 4.7 cm) and were pooled to yield one composite soil sample. The forest floor layer (LFH or O horizon) was removed prior to soil collection. Soil samples were placed in coolers and brought to the laboratory for further analysis. During sample collection and transportation, precautions were taken to avoid soil compaction and to minimize the crushing of soil aggregates.

2.4.2 Aggregate-size separation

The field-moist soil samples were gently broken along natural planes of weakness and passed through a 6-mm sieve before air-drying. Sub-samples (2 x 100 g) of the air-dried soils were wet-sieved using the Kemper technique as described in Angers et al. (2007), giving three aggregate-size classes: >1000 μm fraction (large macro-aggregates), 250-1000 μm fraction (small macro-aggregates) and <250 μm fraction (micro-aggregates and S&C). Briefly, the soil was placed on a set of sieves (250 and 1000 μm) and soaked in deionized water prior to sieving for 10 min to allow slaking, which is the breaking of unstable aggregates due to air and pressure build-up inside the aggregates upon submersion in water. By starting the motor of the wet-sieving apparatus, the sieves were allowed to raise and lower 3.9 cm, 30 times per min for 10 min. Material remaining on the sieves was rinsed into pre-weighed plastic pans. Material passing through the 250 μm mesh was poured into 1 L plastic jars and centrifuged for 15 min at 2000 revolutions/min to discard the excess water. The three aggregate-size fractions were oven-dried at 50°C and weighed.

2.4.3 Density fractionation and aggregate dispersion

Free light fraction (LF) organic matter was separated from the heavy fraction (HF) (i.e., mineral soil) by density flotation following the method described in Gregorich and Beare (2007). Briefly, a sub-sample (20 g) of each of the three different aggregate-size classes was soaked in 1.7 g cm^{-3} sodium iodide (NaI), slowly shaken by hand, and allowed to settle for 48 h before recovering the suspended LF with a vacuum filtration unit equipped

with a 0.45 μm nylon filter. The 1.7 specific gravity is recommended for isolating LF as this density separates most organomineral and mineral particles from free organic materials (Gregorich and Beare 2007). The LF was rinsed using a 0.01 *M* $CaCl_2$ solution and deionized water, oven-dried at 50°C, and weighed. The HF was rinsed as described above and centrifuged for 15 min at 2000 revolutions/min. This rinse-centrifugation cycle was repeated 3 to 5 times, until the supernatant became clear of NaI (uncolored). The HF was oven-dried at 50°C and weighed.

The intra-aggregate particulate organic matter (iPOM) was separated from the silt plus clay fraction (S&C) by shaking the HF on a reciprocal shaker with 100 ml of deionized water and 10 glass beads for 16 h and by passing the dispersed fraction through a 53 μm sieve. The material remaining on the sieve (i.e., iPOM) and the material passing through the 53 μm meshes (i.e., S&C) were oven-dried at 50°C and weighed. Mass and organic C balances of all isolated soil fractions were used to determine recovery efficiency. A graphical representation of the soil fractionation scheme is shown in Figure 2.2.

2.4.4 Soil analyses

Subsamples from all fractions were ground and analyzed for their C and N concentrations by dry combustion using a LECO CHN-1000 analyzer (Leco Corp., St. Joseph, MI, USA). No carbonates were detected in soil samples, thus the C analysis was a measure of total organic C concentration (Carter and Gregorich 2007). The C content of each soil fraction was calculated and data were reported on a whole soil C basis. Cation exchange capacity (CEC) of whole soil was determined by summing exchangeable cations extracted with 0.1 *M* $BaCl_2$ and by atomic-absorption spectrophotometry (Hendershot et al. 2007). The pH was determined in water using a PHM82 pH meter (Radiometer, Copenhagen, Denmark) using a 1:2 soil:water ratio. Soil texture was determined using the standard hydrometer method (Kroetsch and Wang 2007). The C saturation level of the S&C was calculated according to Carter et al. (2003).

2.4.5 Statistical analysis

The data were analyzed using the MIXED procedure of SAS System v.9.1 (SAS Institute Inc., Cary, NC). Forest type and soil properties or size-density fraction were

considered as fixed effects whereas site and replication (nested within site) were considered as random effects. To meet the assumptions of normality and homoscedasticity, the data were log10-transformed (soil properties) or arcsine-transformed (soil size-density fraction). The analysis was weighted (WEIGHT statement) by a measure of tree species composition to minimize the impact of unwanted tree species in a sampling plot. Thus, a "pure aspen" plot containing 100% of aspen had a higher weight than one containing 95% of aspen and 5% of other species (unwanted). Differences between means were tested using orthogonal contrasts (CONTRAST statement). For result presentation, means (estimates) and confidence limits were converted back to the original scale by reversing the transformation. Statistical significance was set up at the 0.05 level, but significant difference at the 0.10 level was also considered given the inherent large variability in forest soils.

2.5 Results

To ensure that potential losses during the fractionation procedure did not introduce bias, the mass and organic C content of the whole soil were compared with the sums of mass and C content in the various fractions to determine recovery efficiency. Calculations of the mass and C balances revealed that recovery efficiency was on average (± 1 SE) 99.3 (± 0.4)% and 95.0 (± 2.0)%, respectively (data not shown). The reproducibility of separation procedures was on average (± 1 SE) 91.9 (± 0.5)% (data not shown).

2.5.1 Whole soil characteristics

Differences in C content and C:N ratio among forest types decreased in the following order: black spruce (46.3 Mg C ha^{-1}, 18.8) > mixedwood (41.9 Mg C ha^{-1}, 16.5) > trembling aspen (34.7 Mg C ha^{-1}, 14.6); no significant difference was found for N content, total C and total N (Table 2.2). Soil pH was significantly higher under aspen (4.7) than under spruce (4.3), and intermediate under mixedwood (4.6). Bulk density, CEC and soil texture were not different among forest types (Table 2.2).

2.5.2 C distribution in the aggregate sizes

Aggregate C content of the mineral soil decreased in the following order: large macro-aggregate (>1000 μm) > small macro-aggregate (1000-250 μm) > micro-aggregate

and S&C (<250 μm) (Figure 2.3). Around 85% of total C content was found in the macro-aggregate fraction (55% in the large macro-aggregate fraction and 30% in the small macro-aggregate fraction), and only 15% was found in the micro-aggregate and S&C. The proportions of total C content within these aggregate size classes were not different among forest types (Figure 2.3). Similar results were found for soil weight partition among aggregate size classes (data not shown).

2.5.3 C distribution in the size-density fractions

The proportions of total C content and the C contents stored (in Mg C ha^{-1}) within size-density fractions were significantly different among forest types (Figures 2.4 and 2.5). In general, more C was found in LF and iPOM under spruce (6.13% or 2.67 Mg C ha^{-1} and 28.94% or 13.32 Mg C ha^{-1}, respectively) than under aspen (3.61% or 1.23 Mg C ha^{-1} and 18.87% or 6.47 Mg C ha^{-1}, respectively), the values under mixedwood being intermediate (4.90% or 2.00 Mg C ha^{-1} and 22.45% or 9.29 Mg C ha^{-1}, respectively). On a proportion basis only, more C was found in S&C under aspen and mixedwood than under spruce (Figure 2.4).

2.5.4 C saturation capacity

The C associated with mineral particles (S&C) was not significantly different from the theoretical capacity of soil C saturation in this fraction (Carter et al. 2003), except for trembling aspen soil where this fraction was significantly lower (Figure 2.6). S&C was saturated at 76%, 84% and 65% of the capacity level under black spruce, mixedwood and trembling aspen, respectively. The C saturation capacity of the soil fine fraction for the study area was estimated at 32.4 g C kg^{-1} (Figure 2.6).

2.6 Discussion

Because permanent site conditions such as drainage, soil texture, topography, stand origin, parent material and soil type were not related to tree species composition (Tables 2.1 and 2.2), the differences observed among soil physical fractions are attributed to the effect of tree species and their associated understory. To the best of our knowledge, this study is the first to specifically address the effect of forest types on SOC stabilization through soil aggregation and soil physical fractions in a natural ecosystem. The very few studies focusing

on this topic took place in managed plantation systems (e.g., Quideau et al. 1998; Blanco-Canqui et al. 2007; Sarkhot et al. 2008; Gama-Rodrigues et al. 2010; Saha et al. 2010), where soil disturbance is high and naturally-associated understory is generally lacking. In addition, the tree species selected in these studies were mostly genetically improved species (e.g., loblolly pine and hybrid poplar clones). Under these relatively artificial conditions, most of these studies reported changes in soil aggregation or in soil physical fractions among tree species composition, even at the genotypic level.

Similarly, our findings highlight the potential of tree species and their associated understories to influence SOC stabilization in the Canadian boreal forest through soil physical fractions. While C distribution in the aggregate size classes was not different among forest types, C distribution among size-density fractions varied significantly. The amounts of C in LF and iPOM were higher under black spruce than other forest types, which was not expected. Because these soil fractions are not intimately bound to mineral particles, they can be defined as uncomplexed organic matter or UOM (*sensus* Christensen 2001). UOM is believed to be less protected against microbial degradation compared with the mineral-associated fraction because it is more accessible to microbes and their enzymes, and usually less recalcitrant biochemically (von Lützow et al. 2006). In soils with permanent vegetation, UOM can represent from 15% to 40% of the SOC stored in the surface soil (Christensen 2001). In our study, UOM accounted for 35%, 27% and 22% of total SOC under black spruce, mixedwood and aspen, respectively. Thus, black spruce forests accumulated more SOC in the less protected soil fractions relative to aspen.

While total SOC contents in the surface mineral layer were higher under black spruce (46.3 Mg C ha^{-1}), followed by mixedwood (41.9 Mg C ha^{-1}) and aspen (34.7 Mg C ha^{-1}), SOC contents associated with mineral particles (S&C) were similar among forest types, i.e., about 30 Mg C ha^{-1}. The mineral-associated fraction has been referred to as passive fraction, owing to the chemical protection of adsorbed soil C at mineral surfaces (Figure 2.1; Six et al. 2002). Together with secondary recalcitrance (e.g., black carbon), chemical protection is among the most efficient stabilization mechanisms for long-term C sequestration, with an estimated mean residence time of hundreds of years in the soil (Trumbore et al. 1996; Torn et al. 1997;

Laird 2001; von Lützow et al. 2006). Therefore, this implies that perhaps a large part of the C stored in this fraction does not originate from the current forest type.

It has been suggested that mineral soils have a limited capacity to store C in the fine fraction (Hassink 1997). According to the C saturation theory, once the capacity level of the mineral-associated pool is reached, extra organic C accumulates in the UOM pool. A number of experiments corroborate this theory (e.g., Hassink 1997; Six et al. 2002; Carter et al. 2003; Gulde et al. 2008). Although these studies were all conducted in agricultural systems, our study may also suggest a finite SOC storage capacity in forest soils, but this remains to be experimentally tested. While black spruce and mixedwood C levels were not different from the calculated C saturation level, the mineral-associated pool of aspen was significantly lower than the theoretical saturation level. Soils that were closer to the saturation level accumulated higher amounts of UOM (i.e., black spruce and mixedwood) compared with soils further away from saturation (i.e., aspen). Admittedly, a large variability may exist around this equation of soil saturation potential although, in relative terms, the results still suggest that black spruce and mixedwood were closer to saturation compared with aspen.

Differences among soil fractions in C distribution and in the soil saturation level reached may originate from differences in SOC mineralization rates between forest types. Furthermore, the higher accumulation of UOM under black spruce may indicate that these forests are characterized by a slower C turnover. Two main reasons may explain different C turnover rates between spruce and aspen. First, C inputs returned to the soil in black spruce forests come primarily from needle and moss litters that decompose slowly in the early stages of decomposition (Van Cleve et al. 1986; Prescott et al. 2000). Spruce litter is acidic, molecular-complex and less palatable for soil decomposers compared with aspen broadleaves, while moss is made of simple but slow-decomposing compounds (Flanagan et Van Cleve 1983; Van Cleve et al. 1986). Second, decomposition rates under spruce are typically slower because of harsh soil conditions limiting microbial activity (Fenton et al. 2005; Lavoie et al. 2005; Laganière et al. 2009). The soil under black spruce is colder than under aspen because light penetration to the forest floor and evapotranspiration capacity is lower, but mainly because the ground cover associated with black spruce (i.e., bryophytes) keeps the soil moist and insulated from thermal variations (Oechel and Van Cleve 1986).

These reasons may explain why more UOM was found under spruce relative to aspen and why soils under aspen were further away from saturation. Ecosystems that have environmental conditions constraining decomposition may have more UOM accumulating than what can be explained by C input alone (Gregorich et al. 2006). Consequently, the higher litter quality and the microclimatic conditions favoring decomposition under aspen may have reduced the amount of C available to enter either in LF, iPOM, the mineral-associated C pool or all three, thus reducing the soil saturation level as well as the amount of UOM.

What might happen to the different SOC pools following climate change is still uncertain and subject to speculation. The potential increase in soil temperature may reduce the environmental constraints on decomposition found under spruce and might cause losses of its extra amount of UOM. Otherwise, the main effect of climate change on SOC dynamics may not originate from changes in precipitation and temperature regimes, but may originate indirectly from variations in tree species composition and distribution (Fissore et al. 2009). If so, the replacement of black spruce with trembling aspen alone would result in a loss of around 25% of the total SOC contained in the surface mineral layer, which is worthy of consideration. In comparison, the conversion of forested lands to agricultural areas results in a depletion of SOC stocks by 30% on average (Laganière et al. 2010a).

2.7 Conclusion

Our results show that SOC stocks in the surface mineral layer were higher under black spruce than under mixedwood and aspen. A higher proportion of the SOC stock under aspen was chemically protected within S&C. On an absolute basis, however, the amounts of chemically-protected SOC did not differ with forest types (around 30 Mg C ha^{-1} each). Instead, the extra amounts of SOC contained in black spruce and mixedwood soils were present in the less protected fractions only (i.e., UOM: LF and iPOM), probably because these forests are characterized by slower C turnover and also because the capacity of these soils to chemically protect SOC on mineral surfaces was nearly reached. These differences in the amounts of SOC stored within soil physical fractions might have strong repercussions on the C budget of the Canadian boreal forest under climate change.

2.8 Acknowledgements

This study was funded through a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Project Research Grant. We acknowledge the support from the Fonds québécois de la recherche sur la nature et les technologies (FQRNT), the Canadian Forest Service, Laurentian Forestry Centre, and the Soils and Crops Research and Development Centre. We are grateful to Gabriel Lévesque, Xavier Cavard, Stephen Hart, Éric Girard, Jessie Parent and Alain Courcelles for their valuable assistance in the field and in the laboratory. We thank Michèle Bernier-Cardou for her statistical assistance and Mark Gillis for providing data from Canada's NFI database.

Table 2.1 Site characteristics of the forest types located in the eastern boreal forest of Canada (n=8). Different lowercase letters denote significant differences at $p < 0.05$ between forest types according to the mixed linear models as described in the Materials and methods section.

Site characteristic	Forest type		
	Spruce	Mixedwood	Aspen
Topography	Flat	Flat	Flat
Stand origin	Wildfire (1916)	Wildfire (1916)	Wildfire (1916)
Climate	Boreal	Boreal	Boreal
Mean annual temperature (°C)[1]	0.7	0.7	0.7
Mean annual precipitation (mm)	890	890	890
Drainage	Moderate	Moderate	Moderate
Parent material	Lacustrine clay	Lacustrine clay	Lacustrine clay
Soil type	Luvisol	Luvisol	Luvisol
Soil texture	Clayey	Clayey	Clayey
Spruce basal area (%)[2]	89.4 ± 4.2a	33.8 ± 3.6b	8.9 ± 1.8c
Aspen basal area (%)	1.8 ± 0.7c	59.5 ± 3.5b	88.5 ± 2.6a
Other species basal area (%)	8.8 ± 4.0ab	6.7 ± 1.6a	2.6 ±2.3b
C stock (t ha^{-1}):[3]			
Forest floor	41.4 ± 2.66a	31.3 ± 1.74b	23.5 ± 1.35c
Mineral soil 0-15 cm	43.9 ± 4.78a	37.0 ± 3.77ab	33.6 ± 3.61b
Mineral soil 15-55 cm	45.4 ± 16.4a	40.5 ± 12.9a	54.9 ± 18.9a

[1]Mean annual temperature and precipitation are from Environment Canada (2010).
[2]Tree basal areas are means ± 1 SE from Cavard et al. (2010).
[3]Forest floor and mineral soil C stocks are means ± 1 SE from Chapter I.

Table 2.2 Soil properties (means and 95% confidence limits) of the 0-15 cm mineral layer under different forest types located in the eastern boreal forest of Canada (n=8). Different lowercase letters denote significant differences at $p < 0.05$ between forest types according to the mixed linear models as described in the Materials and methods section.

Soil characteristic	Forest type		
	Spruce	Mixewood	Aspen
C content (t C ha^{-1})	46.3 (36.6-58.6)a	41.9 (33.1-52.9)ab	34.7 (27.5-43.9)b
N content (t C ha^{-1})	2.47 (2.10-2.90)a	2.54 (2.10-3.08)a	2.37 (2.02-2.79)a
Total C (%)	3.75 (2.45-5.75)a	3.60 (2.24-5.80)a	2.66 (1.74-4.08)a
Total N (%)	0.20 (0.14-0.29)a	0.22 (0.14-0.34)a	0.18 (0.12-0.27)a
C:N ratio	18.8 (17.3-20.5)a	16.5 (15.0-18.2)b	14.6 (13.4-15.9)c
Bulk density (g cm^{-3})	0.82 (0.66-1.02)a	0.77 (0.60-0.98)a	0.87 (0.70-1.08)a
pH (H_2O)	4.33 (4.09-4.58)b	4.58 (4.29-4.90)ab	4.73 (4.47-5.01)a
CEC (cmol(+) kg^{-1})	8.91 (6.80-11.7)a	8.71 (6.33-11.9)a	7.92 (6.03-10.4)a
Sand (%)	10.6 (6.17-13.8)a	13.7 (6.84-21.0)a	13.7 (8.43-18.6)a
Silt (%)	43.4 (37.9-48.7)a	39.8 (34.8-44.8)a	39.2 (33.9-43.7)a
Clay (%)	46.0 (39.6-52.4)a	46.5 (38.8-55.5)a	45.9 (39.5-51.9)a

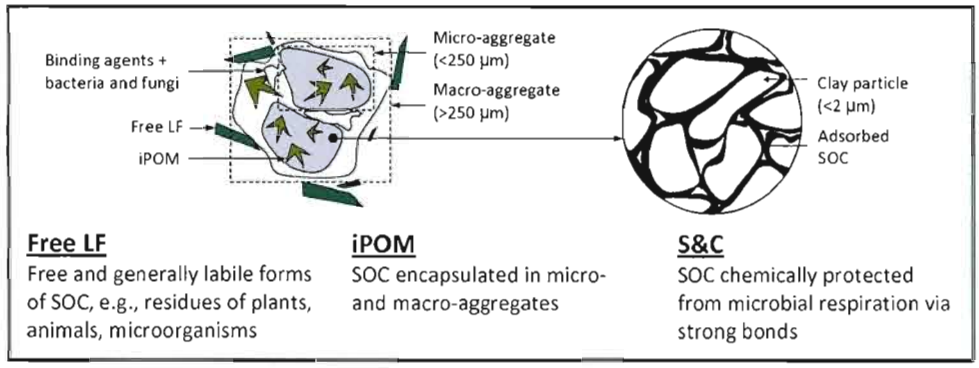

Figure 2.1 Graphical representation and general description of the different soil physical fractions isolated in this study (iPOM, intra-aggregate particulate organic matter fraction; LF, light fraction; S&C, silt plus clay fraction; SOC, soil organic carbon).

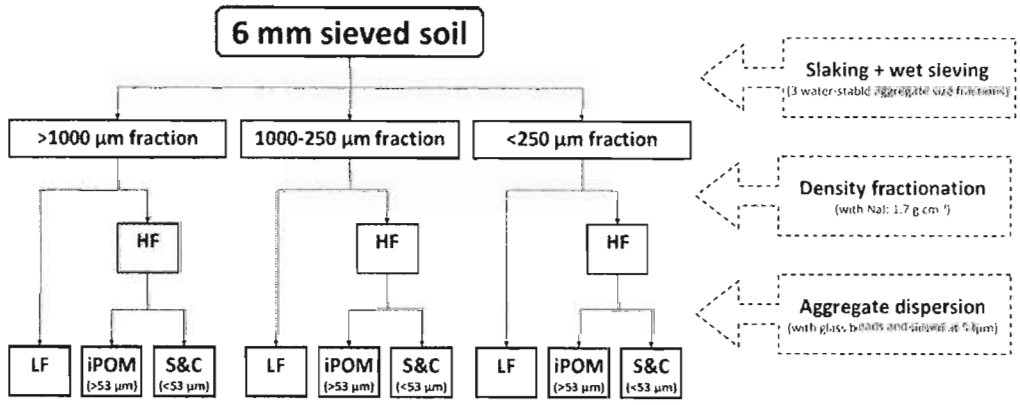

Figure 2.2 Soil fractionation scheme used in this study (HF, heavy fraction; iPOM, intra-aggregate particulate organic matter fraction; LF, light fraction; S&C, silt plus clay fraction).

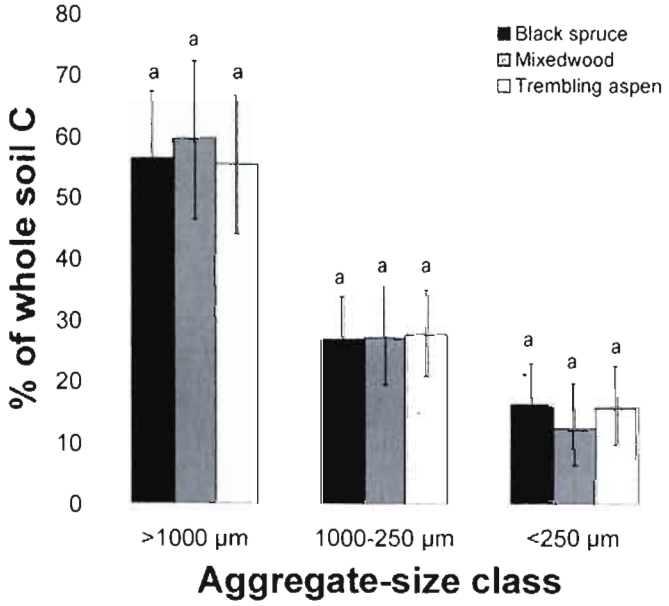

Figure 2.3 Proportions of total C content (means and 95% confidence limits) stored within aggregate size classes among forest types. Different lowercase letters denote significant differences at $p < 0.05$ between forest types according to the mixed linear models as described in the Materials and methods section.

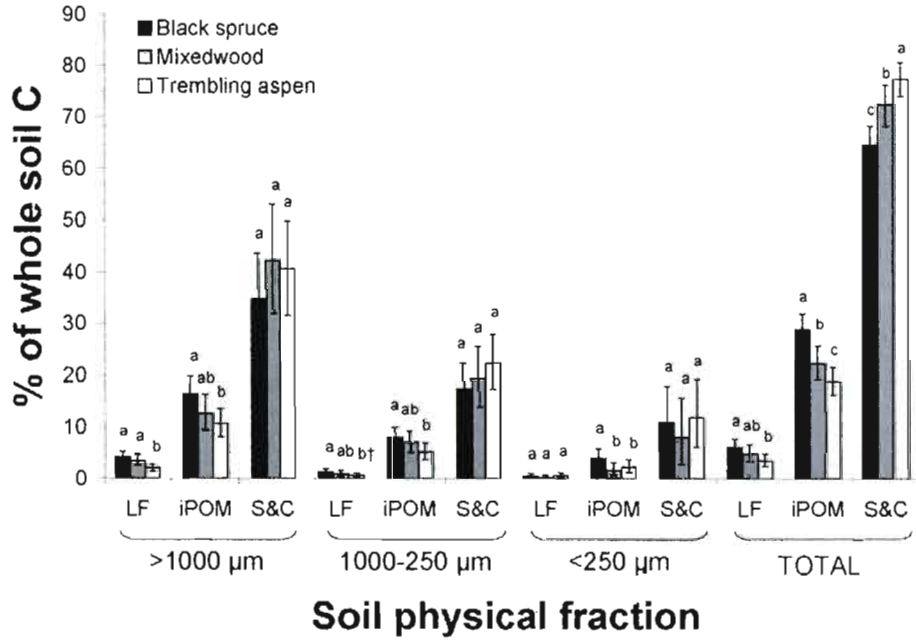

Figure 2.4 Proportions of total C content (means and 95% confidence limits) stored within soil size-density fractions among forest types (iPOM, intra-aggregate particulate organic matter fraction; LF, light fraction; S&C, silt plus clay fraction). Different lowercase letters denote significant differences at $p < 0.05$ (†, $p < 0.10$) between forest types according to the mixed linear models as described in the Materials and methods section.

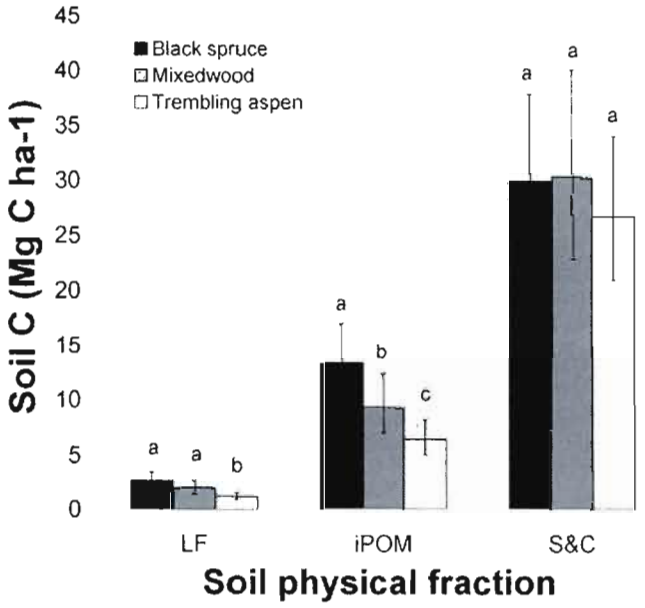

Figure 2.5 C content (means and 95% confidence limits) stored within soil size-density fractions among forest types (iPOM, intra-aggregate particulate organic matter fraction; LF, light fraction; S&C, silt plus clay fraction). Different lowercase letters denote significant differences at $p < 0.05$ between forest types according to the mixed linear models as described in the Materials and methods section.

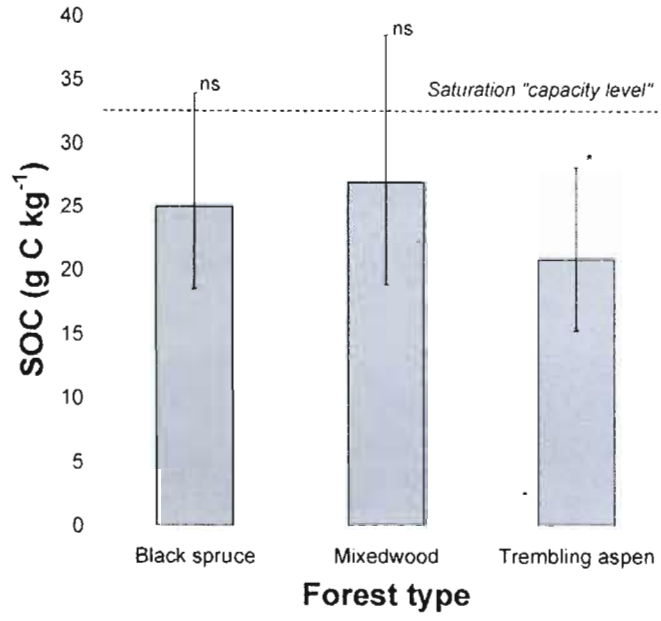

Figure 2.6 Comparison between mineral-associated C (means and 95% confidence limits) among forest types and C saturation level calculated according to Carter et al. (2003) (*, $p < 0.05$; ns, non-significant).

CHAPITRE III

THE EFFECT OF BOREAL FOREST COMPOSITION ON SOIL RESPIRATION IS MEDIATED THROUGH VARIATIONS IN SOIL TEMPERATURE AND C QUALITY

Dans le chapitre précédent, j'ai montré que le C contenu dans le sol minéral différait quantitativement selon la composition forestière, mais aussi au niveau de sa répartition dans les fractions physiques du sol. Il en est ressorti que les sols forestiers se développant sous l'épinette noire possédaient une plus grande quantité de C, mais que ce C était localisé dans les fractions de sol les moins bien protégées physiquement. Dans le présent chapitre, j'essayerai d'établir si l'effet de la composition forestière sur les pertes de COS s'observe également *in situ* et, dans l'affirmative, quels sont les facteurs qui expliquent cette variation entre les types de forêts. Je serai notamment en mesure de savoir si la plus grande accumulation du C dans les sols sous l'épinette noire est bel et bien due à des conditions microclimatiques défavorables et à une qualité biochimique des apports en C limitant les taux de décomposition, comme il avait été suggéré dans les deux premiers chapitres. Cette étude figure parmi les premières à tester les effets de la composition de la forêt boréale sur la respiration du sol *in situ* en utilisant un design expérimental robuste.

Tous les co-auteurs ont contribué à la conceptualisation et à l'élaboration du design expérimental de l'étude et à la révision du présent article scientifique. JL a exécuté la recherche, analysé les données et écrit l'article. La référence de l'article est :

Laganière, J., D. Paré, Y. Bergeron et H.Y.H. Chen. 2011. The effect of boreal forest composition on soil respiration is mediated through variations in soil temperature and C quality. Sera soumis à Soil Biology and Biochemistry.

3.1 Résumé

Une meilleure connaissance des flux de CO_2 émanant des sols forestiers est critique pour accroître notre compréhension du cycle du C planétaire. Nous avons exploré l'influence de deux espèces d'arbres communes à la forêt boréale, soit en forêts pures (EPN, épinette noire; PET, peuplier faux-tremble) ou en forêts mixtes (FM, mélange EPN-PET), sur la respiration total (R_S), la respiration hétérotrophe (R_H) et la respiration autotrophe (R_A) et leur relation avec la température et l'humidité du sol, la proximité des arbres, le C organique du sol (COS) total et très labile, et le contenu en racines. Des modèles de respiration du sol spécifiques à chaque peuplement ont été développés pour estimer les flux annuels de CO_2 émanant du sol. La température du sol était le facteur principal expliquant la R_S et ses composantes, suivis du COS très labile et total. Ces variables étaient affectées significativement par la composition forestière, alors qu'aucune variation dans l'humidité du sol, la proximité des arbres et le contenu en racines n'a été observée entre les types de forêts. La R_S et la R_H annuelles étaient significativement plus faibles dans EPN que dans FM et PET, alors que la R_A annuelle était plus élevée dans EPN et FM que dans PET. La sensibilité à la température (Q_{10}) de la R_S et la R_H était significativement plus élevée dans EPN que dans FM et PET, suggérant que EPN pourrait libérer plus de CO_2 sous l'effet du réchauffement climatique que les autres types de forêts. Nos résultats suggèrent que la composition de la forêt boréale affecte les flux de CO_2 émanant du sol et que cet effet serait exprimé via des variations dans la température du sol et via d'autres facteurs influençant l'accumulation du COS comme la qualité des apports en C.

3.2 Abstract

Getting a better understanding of CO_2 efflux from forest soils is critical for increasing our comprehension of the global carbon cycle. We explored the influence of two common boreal tree species, either in pure stands (BS=black spruce; TA=trembling aspen) or in mixtures (MW=BS+TA mixedwood), on total (R_S), heterotrophic (R_H) and autotrophic soil respiration (R_A) and their relationship with soil temperature and moisture, tree proximity, very labile and total soil organic C (SOC), and root content. Stand-specific soil respiration–temperature models were developed to estimate annual soil CO_2 efflux. Soil temperature was the main factor explaining R_S and its components, followed by fast and total SOC. These three variables were significantly affected by forest composition, while no variation in soil moisture, tree proximity and root content were observed between stand types. Annual R_S and R_H were significantly lower in BS than in MW and TA, whereas annual R_A was greater in BS and MW than in TA. Temperature sensitivity (Q_{10}) of R_S and R_H was significantly higher in BS than in MW and TA, suggesting that BS could release more CO_2 under climate warming than the other stand types. Our results suggest that boreal forest composition affects soil CO_2 efflux and that this effect would be mediated through variations in soil temperature and through other factors affecting SOC accumulation, including C input quality.

3.3 Introduction

Boreal forest ecosystems hold a major part of the global terrestrial carbon (C) and, unlike warmer ecosystems, boreal soils in general contain a much greater share of it than the vegetation (Lal 2005). Soil respiration (R_S) is a major contributor to atmospheric CO_2; thus, it is important to quantify CO_2 efflux from forest soils and to understand how it is affected by forest management and climate change (Lorenz and Lal 2010). Climate change can have direct effects on R_S by bringing changes to the soil temperature regime and by affecting the importance and duration of the period during which the soil is above the freezing point (IPCC 2007; Mellander et al. 2007). It can also have indirect effects by bringing changes to disturbance regimes that may have an impact on vegetation composition (Bond-Lamberty et al. 2007; Soja et al. 2007).

R_S is the sum of autotrophic respiration (R_A) produced by living roots and their associated rhizosphere (i.e. mycorrhizae and rhizosphere bacteria) and heterotrophic respiration (R_H) generated by microbial decomposition of soil organic matter. Because R_A and R_H are mediated by different organisms and involve different C sources and qualities as well as different processes (Kuzyakov 2006; Subke et al. 2006; Epron 2009), their response to changes in environmental conditions may differ. However, the contrasting results reported in a number of publications illustrate the lack of a mechanistic understanding of this process (Lin et al. 1999; Lavigne et al. 2003; Subke et al. 2006; Zhou et al. 2007; Schindlbacher et al. 2009; Wei et al. 2010).

Soil temperature is recognized as the main factor regulating R_S while soil moisture is secondary, its control over R_S being mostly effective under extreme moisture values (Conant et al. 2004; Luo and Zhou 2006; Li et al. 2008; Litton and Giardina 2008; Wang et al. 2011b). Besides these two major environmental factors, several other variables were shown to affect R_S and its components (i.e. R_H and R_A), including the size of the soil organic C (SOC) pool, the quality of organic matter, the abundance of roots, and the distance from the nearest tree stem (Saiz et al. 2006; Wang et al. 2010b; Luan et al. 2011). Since all these variables are singularly affected by the nature of the forest cover (De Deyn et al. 2008), R_S, R_H and R_A should differ with forest composition.

Previous studies measuring field soil respiration among different stand types are rare (e.g. Borken and Beese 2005; Wang et al. 2011a; Yohannes et al. 2011), and the few that exist were often not designed specifically to isolate the effect of forest composition. For example, Wang et al. (2010b) compared soil respiration rates in three forest types in China where some variables, including stand age and land management, were not fixed. Jonard et al. (2007) measured R_S in pure and mixed stands of oak and beech in Belgium, but the lack of replications did not make it possible to test for differences between stand types. To our knowledge, no studies have investigated the impact of boreal forest composition on field soil respiration and its components in spite of growing evidence that tree species affect soil processes (Binkley and Valentine 1991; Wardle et al. 1997; Binkley and Giardina 1998; Reich et al. 2005; Vesterdal et al. 2008; Laganière et al. 2011).

In this study, we used a replicated block design under natural conditions to explore the influence of two common boreal tree species (one conifer, black spruce *Picea mariana* Mill. BSP, and one broadleaf, trembling aspen *Populus tremuloides* Michx.), both in single-species stands and in mixture with the other species, on soil respiration (R_S, R_H and R_A) and their relationship with soil temperature and moisture, tree proximity, very labile and total SOC, and root content in the Abitibi-James Bay region of eastern Canada. Because permanent site conditions such as climate, soil type and texture, drainage, topography, and time since fire were not related to tree species composition (Jenny 1994), variations in dependent variables were attributed to the effect of tree species and their associated understory.

3.4 Materials and methods

3.4.1 Study area and design

The study area is located in the eastern Boreal Shield of Canada, in the Abitibi-James Bay region of Quebec (49°08' to 49°11'N, 78°46 to 78°53'W). This region is part of the black spruce-feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) forest of western Quebec (Grondin 1996). This domain extends over the Clay Belt region of Quebec and Ontario, a major physiographic region resulting from the deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse, during the Wisconsinan glacial age

(Vincent and Hardy 1977). A large part of this region is characterized by homogeneous site conditions, i.e., a flat topography, a fine-textured parent material, and grey Luvisol as the main soil type (Soil Classification Working Group 1998). The dominant type of disturbance is large fires that kill all aboveground vegetation. The climate is boreal with a mean annual temperature of 0.7°C and annual precipitation of 890 mm (Environment Canada 2010).

Eight mature forest sites dominated by black spruce and trembling aspen, each ranging from pure stands to a variety of mixtures of both species, were selected for the study. These sites were located in an area of 36 km^2 with a maximum distance of 7 km between sites. At each site, three 400 m^2 sampling plots were randomly established: one dominated by black spruce (referred to as BS), one dominated by aspen (TA), and the third one mixed uniformly with both tree species (MW). The understory plant communities typically growing below the forest canopy of a given tree species (i.e. associated understory) and generally consisting in herbs, shrubs and bryophytes were similar within a stand type. The vegetation under spruce canopy included mainly Labrador tea (*Ledum groenlandicum* Oeder), *Vaccinium* spp., and feathermoss (*Pleurozium schreberi* (Bird.) Mitt.); the latter was the dominant ground cover and an important input of organic matter to the soil (Bisbee et al. 2001). The aspen understory included shrubs (*R. pubescens*, *Diervilla lonicera* Mill., and *Viburnum edule* (Michx.) Raf.) and herbs (*C. canadensis*, *Viola* spp., *L. borealis*, and *M. canadensis*) while the mixedwood understory comprised a mixture of the vegetation found under spruce and aspen. The sampling plots were separated by a distance of 40-100 m to minimize variability within a site. Within each plot, the species and diameter at breast height (dbh) were determined for all trees with a diameter >5 cm to estimate tree species basal area and their contribution (%) to total basal area (Table 3.1). All stands originated from the same fire that occurred in 1916 (Légaré et al. 2005a).

During the selection of the sites, particular attention was given to ensuring the similarity of the following permanent site conditions: climate, soil type and texture, parent material, drainage, topography, and time since fire. Furthermore, all selected stands were >1 ha in area, fully stocked and visually homogeneous in structure and composition. More information on stand characteristics is found in Cavard et al. (2010; 2011) and Brassard et al. (2011).

3.4.2 Soil respiration measurements

In each plot, three 1 m^2-microplots were established, in which two polyvinyl chloride collars were inserted into the soil: one 5 cm deep collar (10 cm diam.) to measure total soil respiration (R_S) and one 30 cm deep collar to exclude small roots and measure heterotrophic soil respiration (R_H) as described in Vogel and Valentine (2005). All collars (2 collar types x 3 replicates x 22 plots = 132 in total) were installed after complete soil thawing, in early June 2007, and the first efflux measurement took place 2 weeks after collar insertion to minimize the response of severed fine root decomposition. R_S and R_H were measured during the growing season once a month from June to September 2007, once a week in October 2007, and once in June 2008. We quantified autotrophic respiration (R_A) by comparing soil respiration measured in the collars that excluded roots with those that did not.

CO_2 efflux from soil was measured by placing the soil chamber (LI-6400-09) of a portable infrared gas analyzer (LI-6400, LI-COR Inc., Lincoln, NE) above the collar. While CO_2 efflux was being measured, soil temperature at a depth of 5 cm was recorded with a thermocouple and soil moisture (i.e. volumetric water content, % v/v) was recorded with a TDR-300 time domain reflectometry moisture probe (Spectrum Technologies Inc., Plainfield, IL). On a few occasions, soil moisture inside some root-exclusion zones was greater than in the surrounding soil; thus, data from this zone was excluded to avoid methodological bias. Temperature was also recorded every 4 h from June 2007 to June 2009 using DS1921G iButtons temperature loggers (Maxim Integrated Products Inc., Sunnyvale, CA) inserted at a depth of 5 cm into the soil of each plot. Temperature data were used to estimate soil respiration outside measurement periods using flux-temperature relationships (see details below) and to evaluate annual soil CO_2 efflux as in several other experiments (e.g. Lavigne et al. 2003; Zhou et al. 2007; Wang et al. 2010b). Gabriel and Kellman (2011) demonstrated that for the soil moisture conditions present in most sites of the study region (eastern Canada), flux-temperature relationships alone can be used to reasonably estimate soil CO_2

efflux since moisture exerts a more important control on soil respiration during extreme events only.

Moss was not removed to avoid disturbing the underlying soil. Given that the moss carpet typically associated with conifers may contribute to soil respiration and/or alter CO_2 diffusion from the soil to the atmosphere relative to a soil devoid of mosses, such as in broadleaved stands, we compared soil respiration from five zones where the moss layer (living part) was carefully removed by hand with that from five adjacent zones where the moss layer was kept intact. Our results indicate that the presence of moss in plots containing black spruce (BS and MW) did not significantly alter soil CO_2 efflux during the growing season, nor did it introduce bias in the measurements ($p>0.05$). Average (±SE) soil respiration from June to October 2007 was 3.59 (±0.26) and 3.63 (±0.35) μmol CO_2 m^{-2} s^{-1} for treatment with and without mosses, respectively.

To test whether potential variations in the soil thermal regime between black spruce and aspen stands may originate either from a difference in light penetration (e.g. different canopy characteristics) or from a difference in forest floor thermal properties (e.g. different insulation capacity and specific heat), or both, we performed a forest floor reciprocal transplant experiment. Briefly, 9 forest floor layer samples (20 cm x 20 cm x depth) were extracted from each single-species plot (BS and TA) of one block (Block 9). Three of these samples were transplanted to the sampling locations of the other plot (i.e. spruce forest floor in the aspen plot and vice-versa), three of these samples were discarded to expose the bare mineral soil, and the remaining three samples were placed back to their initial sampling locations to act as controls. Soil temperature was monitored during 1 year using iButtons temperature loggers inserted 5 cm deep into the mineral soil.

3.4.3 Soil sampling and analyses

In each microplot, the forest floor layer (i.e. O horizon) was collected using a sharp knife and a trowel in a 15 cm x 15 cm block while the surface mineral layer (0-15 cm) was carefully extracted using a metal corer (diam: 4.7 cm). The field-moist soil was passed through 6- and 4-mm sieves for the forest floor and mineral layers, respectively, before air-drying and weighing to determine soil bulk density according to Carter and Gregorich (2007).

Roots were removed by hand, weighed and reported in Mg d.m. ha^{-1}. Soil samples were ground and analyzed for their C concentrations by dry combustion using a LECO CNS-2000 analyzer (Leco Corp., St. Joseph, MI, USA) and then reported in Mg ha^{-1}. Soil texture was determined using the standard hydrometer method (Kroetsch and Wang 2007). Similarity of drainage class, parent material and soil type was verified by digging a soil pit (ca. 1 m^3) in each sampling plot (Soil Classification Working Group 1998). The proportions of very labile SOC, indicative of a high-quality organic matter (fast turnover), were taken from the laboratory incubation experiment performed in Chapter I. Briefly, the proportion of very labile SOC corresponded to the proportion of total C respired from the forest floor layer after 100 days of incubation at 29°C under constant moisture (referred to as "fast C" for all soil layers in Chapter I).

3.4.4 Data analysis

To determine the contribution (significance) of environmental factors to explaining variations in soil respiration taken from field measurements, data were analyzed using the MIXED procedure of SAS System v.9.2 (SAS Institute Inc., Cary, NC). Soil temperature, soil moisture, tree proximity, fast SOC, total SOC, and root content were considered as fixed effects whereas block and microplot (nested within block) were considered as random effects. The same procedure was used to explore the effect of tree species composition on soil respiration and environmental variables, but with stand type as a fixed effect. To meet the assumptions of normality and homoscedasticity, the data were log10-transformed when necessary.

Soil temperature data recorded during the field respiration measurements were used to model the relationship between soil respiration and temperature and develop stand-specific soil respiration models. Continuous soil temperature data extracted from data loggers were then used to estimate annual soil CO_2 efflux from all stands. To fit soil respiration data with temperature, we used a two-parameter exponential model that is commonly used in field soil respiration studies (e.g. Lavigne et al. 2003; Zhou et al. 2007; Wang et al. 2010b):

$$[1]\ R = ae^{b(T-10)}$$

where R is the measured soil respiration, R_S or R_H (μmol CO_2 m^{-2} s^{-1}), T is soil temperature (°C) at a depth of 5 cm, a is the mean respiration rate at 10°C, and b is the rate of change in R with a unit change of T. The b values were also used to calculate Q_{10}, which is the temperature sensitivity of soil respiration (i.e. the factor by which the respiration rate increases with a 10°C rise):

$$[2]\ Q_{10} = e^{10b}$$

Annual respiration was estimated by summing daily soil respiration calculated with the following equation (Lavigne et al. 2003):

$$[3]\ \text{annual } R = \Sigma_{daily}\ ae^{\ b(T-10)}\ 3600\ (12/1\ 000\ 000)$$

where T is the average soil temperature at 5 cm depth, recorded 6 times a day, a and b are constants as described above, multiplying by 3600 converts time from seconds to hours, multiplying by (12/1 000 000) converts C from micromoles to grams, and the summation was performed for each day of the year.

The significance of the effect of stand type on modeled soil respiration estimates was tested using linear mixed-effect models as described above. Statistical significance was set up at the 0.05 level, but significant difference at the 0.10 level was also considered given the inherent large variability in forest soils.

3.5 Results

3.5.1 Contribution of environmental variables to explaining soil CO_2 efflux

As shown by the greatest *F* value, soil temperature was by far the main factor explaining R_S and its components, followed by the proportion of very labile SOC and then by the total SOC content for R_S and R_H (Table 3.2). Soil moisture was also a significant predictor for R_S, R_H and R_A while root content was significant for R_S and R_H but not for R_A. The distance from the nearest tree stem (i.e. tree proximity) was significant for R_H only.

3.5.2 Data and parameters of models

The data recorded during field measurements (June 2007 to June 2008) encompassed a wide range of temperature (from 2.2 to 17.6°C) and soil CO_2 efflux in g CO_2 m^{-2} s^{-1} (from 0.78 and 1.31 to 10.90 and 10.27 for R_S and R_H, respectively) that was necessary to model annual soil CO_2 efflux accurately (Table 3.3). The range of temperature for which we measured soil CO_2 efflux represented 80% of the annual temperature range recorded by continuous measurements (data not shown). The relationship between R_S and R_H rates and soil temperature was well fitted by the two-parameter exponential model ($p<0.001$).

Values of model parameters averaged by stand type showed that the relationship between soil respiration (R_S and R_H) and temperature is influenced by forest composition (Table 3.4). Values of respiration parameter "a" were lower in BS than in MW and TA while the reverse was true for temperature parameter "b". The temperature sensitivity (Q_{10}) of R_S and R_H derived from Eq. [2] was greater in BS (2.61 and 2.70) than in MW (2.23 and 1.94) and TA (2.07 and 2.04). No differences in Q_{10} values were observed between R_S and R_H.

3.5.3 Effect of forest composition on modeled soil CO_2 efflux

Mean R_S and R_H rates (in g CO_2 m^{-2} s^{-1}) were significantly lower in BS (2.67±0.17 and 2.39±0.12) than in MW (3.84±0.17 and 3.47±0.12) and TA (3.56±0.16 and 3.46±0.11), whereas no differences were detected for R_A (Table 3.5). The estimated contribution of R_A to R_S was less than 15% on average.

Similar to respiration rates, average annual R_S and R_H (in g C m^{-2} yr^{-1}) were significantly lower in BS (1020±64 and 905±46) than in MW (1462±64 and 1315±46) and TA (1353±60 and 1313±43). Average annual R_A was significantly higher ($p<0.10$) in BS and in MW than TA. Annual contribution of R_A to R_S was also estimated at less than 15% on average.

3.5.4 Effect of forest composition on environmental variables

Continuous soil temperature recorded from May 15 2007 to May 15 2009 varied well across seasons and, to a lesser extent, among stand types (Figure 3.1). Evidently, the highest

soil temperatures occurred during summer, although soils were still fairly warm in October (i.e. >5°C). From December to May, soil temperatures were quite constant, at around 0°C. Average soil temperature was 4.7, 4.9 and 5.2°C in BS, MW and TA, respectively (Table 3.1). In the forest floor transplant experiment, we found that the average soil temperature in the mineral soil was also lower in BS (Figure 3.2). In addition to the stand type effect, the type of substrate (i.e. spruce forest floor, aspen forest floor or bare mineral soil) had a significant influence on soil temperature as well as the stand type x substrate interaction. In the BS plot, the greatest mean annual temperature was found below the spruce forest floor while in the TA plot, the greatest one was found below the aspen forest floor.

In addition to soil temperature, forest composition influenced the amount and the quality of SOC (see also Chapter I). The proportion of very labile SOC was lower in BS (6%) than in MW (10%) and TA (10%) and was inversely related to total SOC content (86, 71 and 62 Mg C ha^{-1}, respectively). Soil moisture, tree proximity, root content and very labile SOC reported on an areal basis did not differ between stand types.

3.6 Discussion

R_S and its components (R_H and R_A) were significantly affected by forest composition. Greater R_H rates and annual cumulative CO_2 losses from R_H were found in stands containing aspen (i.e. TA and MW) than in single-species BS stands, whereas greater annual R_A was found in stands containing black spruce (i.e. BS and MW) than in TA. To our knowledge, this field experiment is among the first attempts to investigate the effect of boreal forest composition on components of soil respiration using a replicated block design under natural conditions. Because our sites were selected on the basis of similar soil permanent conditions (see Jenny 1994), these differences in soil CO_2 efflux are attributable to the influence that a tree species and its associated understory vegetation has on the soil environment (Binkley and Valentine 1991; Wardle et al. 1997; Binkley and Giardina 1998; Reich et al. 2005; Vesterdal et al. 2008; Laganière et al. 2011).

When added to the fixed-effect part of the model with environmental variables (i.e. soil temperature, soil moisture, tree proximity, etc.), however, stand type had no significant effect on soil respiration (data not shown). Therefore, the effect of stand type on soil respiration that

was observed in this experiment would have been mediated through one or more environmental variables that were already included in the model. Since soil moisture and tree proximity did not differ among stand types, soil temperature as well as fast and total SOC would have been responsible for the variation in soil respiration among stand types.

3.6.1 Heterotrophic respiration

Soil temperature was the main factor driving soil respiration and it was correlated to the observed differences in R_H between stand types. The colder soil of black spruce stands reflected the lower R_H (mean rates and annual estimates) estimated in these stands. Higher light interception by conifers canopy relative to aspen (Messier et al. 1998) and the development of a thick moss carpet with a high water content under black spruce (requiring more heat to increase soil temperature) likely contributed to lower soil temperature (Fenton et al. 2005; Lavoie et al. 2005), as exemplified by the forest floor transplant experiment we performed (Figure 3.2). However, temperature would not be the only factor influencing R_H among stand types. The organic matter produced by each tree species and their associated understory contains various proportions of nutrients, lignin and secondary metabolites that determine the quality of organic matter and rates of decomposition (Berg 2000; Preston et al. 2000). As shown by the proportion of very labile SOC (Table 3.1), the forest floor organic matter from aspen stands contained more rapidly-released C than that from black spruce, suggesting that the organic matter produced by aspen is of higher quality (i.e. less biochemically recalcitrant). This high-quality organic matter thus contributes to hasten the organic matter turnover rate in aspen stands and to lower SOC contents compared with black spruce (Table 3.1).

Differences in SOC quality are also expected to lead to different temperature sensitivities of R_H according to simple thermodynamic laws (Davidson and Janssens 2006). The greatest increase in CO_2 efflux upon warming was found in black spruce soils (i.e. Q_{10}=2.70). Likewise, in a previous soil warming experiment conducted under controlled conditions, the greatest R_H sensitivity to warming was also found in BS forest floor relative to that from MW or TA (see Chapter I). According to the temperature sensitivity vs. recalcitrance theory (Conant et al. 2008; Wetterstedt et al. 2010; Xu et al. 2010), the greater

Q_{10}s observed in black spruce soils would imply a lower C quality (i.e. higher recalcitrance), which is in agreement with what we found (as measured by the proportion of very labile SOC) and what many others have found (e.g. Flanagan and Van Cleve 1983; Trofymow et al. 2002).

However, when reported on an areal basis (in Mg ha^{-1}), very labile SOC did not differ between stand types. In line with the results reported in Côté et al. (2000), we found that an inverse relationship between total SOC content and the proportion of very labile SOC cancelled the effect of SOC quality on soil CO_2 efflux (Table 3.1). However, since the laboratory incubation method used to estimate SOC quality did not reflect *in situ* conditions, the proportion of very labile SOC did not take into account stand-specific environmental constraints to R_H. Harsher soil conditions in black spruce stands would thus favour accumulation of labile SOC. In line with this, Laganière et al. (2011; Chapter II) performed a soil physical fractionation analysis that separated SOC into fractions differing in stability. They found more SOC stored in black spruce than in aspen stands but this extra SOC was located in the less protected (labile) fractions. Therefore, an increase in average soil temperature induced by climate change might reduce the temperature limitation to R_H and make more labile SOC available to decompose, as suggested in previous studies (Neff and Hooper 2002; Davidson and Janssens 2006; Laganière et al. 2011). However, by putting the soil temperature regime of aspen stands into the flux–temperature models developed for black spruce stands (Table 3.4), the simulation shows that the mean (±SE) annual R_H from black spruce stands was still far below that of aspen stands (R_H=955 ± 27 vs. 1313 ± 43 g C m^{-2} yr^{-1}), indicating that a soil warming much greater than the 0.5°C difference between spruce and aspen mean annual soil temperature would be required to observe a dramatic change in black spruce annual R_H.

3.6.2 Autotrophic respiration

The only environmental factor influencing autotrophic respiration among stand types was soil temperature, and it was negatively related in such a way that R_A was greater in colder soils, i.e. in stands containing black spruce (BS and MW). However, this idea that R_A would be greater in colder than in warmer soils remains unlikely since many studies have

shown the opposite (Lavigne et al. 2003; Vogel et al. 2005; Schindlbacher et al. 2009). For example, in a climatic gradient of balsam fir stands in eastern Canada, Lavigne et al. (2003) found R_A to be around four times lower in colder than in warmer sites (for a 2°C difference in mean annual soil temperature). Hence, this difference in R_A between stand types may probably originate from a difference in root anatomy, physiology and allocation strategy between tree species. Tree species strongly influence root dynamics and, compared with deciduous tree species, evergreen ones usually have higher belowground C allocation (Gower et al. 1995; Vogt et al. 1996; Litton et al. 2007). In line with this, Steele et al. (1997) found fine root net primary production estimated by minirhizotrons to be higher in black spruce than in aspen stands in central Canada. This may explain the greater R_A observed in stands containing black spruce.

Our annual R_A estimates were similar to those found by O'Connell et al. (2003) in two black spruce stands of central Canada (annual R_A=55 and 124 g C m^{-2} yr^{-1}). Reported on R_A contribution to R_S, these values were slightly greater (i.e. 17 and 22%) than what was observed in this study (i.e. 4-14%). However, previous studies reported such high variability in R_A to R_S estimates that root respiration may account for 5-90% of total soil respiration in forest ecosystems (Hanson et al. 2000; Bond-Lamberty et al. 2004). In addition, the lowest contributions of R_A to R_S were generally found in boreal forests (Subke et al. 2006). Our R_A estimates are thus on the lower end of the range. The method may partly explain these low R_A values (see the "Methodological considerations" section) as well as the potential overestimation of winter R_S (that may have lowered the R_A/R_S ratio) because no field measurements were taken during this period.

3.6.3 Modeling winter soil CO_2 efflux

When models are used to predict values outside the limit of measured data used to build the relationship, some bias may arise (Bond-Lamberty et al. 2004). The range of soil temperatures covered during our soil CO_2 efflux measurements represented 80% of the soil temperature range throughout the year (the remaining 20% being on the lower end). As in many studies, we lack soil CO_2 efflux measurements for colder temperatures (<2°C), a period corresponding to the winter season (the snow-covered period). In our study, the mean soil

CO_2 efflux rate during that period was roughly 1.4 g CO_2 m^{-2} s^{-1} in BS and 2.3 g CO_2 m^{-2} s^{-1} in TA and MW (Figure 3.1). These values seem high compared with those of studies that measured soil CO_2 efflux under winter conditions since CO_2 efflux below 1.0 g CO_2 m^{-2} s^{-1} is generally found (Vogel et al. 2005; Sullivan 2010; Wang et al. 2010a). However, the soils in our study were warmer during winter compared with those of these other studies, in which soils reached -14°C in some cases. Soil temperature in our stands during winter was close to 0°C and soil CO_2 efflux was more comparable to that reported in coniferous stands of central (O'Connell et al. 2003) and eastern Canada (Lavigne et al. 2003). The latter two studies reported R_S values between 0.2 and 2.2 g CO_2 m^{-2} s^{-1} at around 0°C. Moreover, the contribution of winter soil respiration (December to May; R_S and R_H) estimated by our models was 25% on average (data not shown), which is well within the 5-40% range of annual soil CO_2 efflux reported in other studies conducted in boreal ecosystems (O'Connell et al. 2003; Bond-Lamberty et al. 2004; Wang et al. 2010a). Therefore, we assume that the behaviour of our models at low temperatures was satisfying and that they provided reasonable estimates.

3.6.4 Non-additive effect in mixedwoods

The highest soil CO_2 efflux (mean rates and annual cumulative R_S) was found in mixed aspen-black spruce stands. MW had the greatest CO_2 losses from R_H along with TA, and the greatest CO_2 losses from R_A along with BS. Hence, having aspen and black spruce in a mixture caused a synergistic (non-additive) effect on R_S and its components. Since the mean annual soil temperature of MW was intermediate (additive) compared with that of single-species stands (BS and TA), another factor than temperature could explain the greatest R_S values found in MW. It has been suggested that the presence of one tree species could improve the growth or any other process (such as decomposition) of the other species (Hooper et al. 2005). Non-additive facilitative effects of litter mixing on decomposition rates are common (Gartner and Cardon 2004; Hättenschwiler et al. 2005). In this case, the higher C quality provided by aspen litter may in fact have increased the decomposition rates of low-quality C from black spruce and resulted in greater R_H than what is expected from both single-species stand values. The facilitative effect of aspen litter on black spruce organic matter decomposition is well documented (Légaré et al. 2005b; Laganière et al. 2009, 2010b).

Moreover, the non-additive response of R_A could be explained by niche differentiation, a theory stating that a stand composed of functionally divergent species (i.e. with complementary traits) uses the resources (light, water and nutrients) more efficiently and can achieve higher productivity than monocultures of the same component species (Hooper et al. 2005). Higher annual R_A in MW may thus be related to differences in fine root productivity and spatial distribution, which is similar to what Brassard et al. (2011) observed in aspen-jack pine mixtures in northwestern Ontario, Canada.

3.6.5 Methodological considerations

A potential bias of the small root exclusion (SME) method would be that the root exclusion collar only excludes roots from the top forest floor layer to less than 30 cm into the soil. While roots in northern forests are highly concentrated in the organic and upper mineral soil layers (Brassard et al. 2009), some roots below this threshold may have contributed to R_H and inflated its value. Nevertheless, by using this method, we eliminated some artefacts brought by other techniques, including changes in microenvironmental conditions (soil temperature and moisture) related to canopy openness brought about by tree mortality either when cutting the shoot (clear-cut vs. control method) or girdling its phloem (tree girdling method), as well as the spatial bias that comes from placing the root exclusion collars in a relatively large treeless area (e.g. 3 m x 3 m) when using the large root exclusion (LRE) method. Moreover, when using the SRE method, a very short period of time is necessary to allow for the extraordinary decomposition generated by the excised roots as opposed to the LRE method. According to Vogel and Valentine (2005), a single week after the insertion of SRE collars is generally needed to obtain soil CO_2 efflux values similar to those found in large trenched plots sampled 10 months after installation. Nevertheless, no perfect and easy method exists for partitioning the components of soil respiration since the manipulation of one component usually leads to changes in respiration from another component. The importance is to be aware of the limitations of each method.

3.7 Conclusion

Soil respiration and its components were significantly influenced by forest composition in the Canadian boreal biome. This influence would be mediated through

variations in soil temperature among stand types and through the quality of the organic matter produced (proportion of very labile C) and the amount of SOC accumulated (total SOC contents).

Moreover, our results suggest that CO_2 efflux from black spruce soils could be increased more under climate warming than that from aspen or from mixed aspen-black spruce soils since the greatest temperature sensitivity of R_H was found in black spruce stands. Given that black spruce is the most widespread tree species in the Canadian boreal biome (Canada's NFI 2010) and that large amounts of C are sequestered in its soil, this finding has implications for predicting the feedback of boreal SOC stocks to climate change.

Collectively, our results highlight the need to consider forest composition in the effort to understand and predict the impact of climate change on soil C dynamics. Therefore, tree species effects should be more adequately represented in ecosystem models.

3.8 Acknowledgements

This study was funded through a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Project Research Grant. We acknowledge the support from the Fonds québécois de la recherche sur la nature et les technologies (FQRNT) and the Canadian Forest Service, Laurentian Forestry Centre. We are grateful to Luc St-Antoine, Jessie Parent, Jessica Lagacé Banville and Thalia Soucy Giguère for their valuable assistance in the field. We thank Michèle Bernier-Cardou for her statistical assistance as well as Pamela Cheers and Isabelle Lamarre for editing the manuscript.

Table 3.1 Stand characteristics (mean ± SE). Significant differences among stand types are denoted by different letters ($p<0.05$).

Variables	BS (n=7)	MW (n=7)	TA (n=8)
Soil temperature (°C)[1]	4.70 ± 0.11b	4.86 ± 0.10ab	5.22 ± 0.10a
Soil moisture (% v/v)	33 ± 3a	32 ± 3a	32 ± 3a
Tree proximity (m)	1.4 ± 0.2a	1.5 ± 0.2a	1.6 ± 0.2a
Root content (Mg d.m. ha^{-1})[2]	19 ± 4a	18 ± 4a	23 ± 4a
Soil carbon:			
Total C content (Mg C ha^{-1})[2]	86 ± 7a	71 ± 7b	62 ± 6b
Percent of very labile C (%)[3]	6 ± 1b	10 ± 1a	10 ± 1a
Content of very labile C (Mg C ha^{-1})[3]	2.6 ± 0.2a	2.9 ± 0.2a	2.3 ± 0.2a
Tree species composition (% basal area):			
Picea mariana	91 ± 3a	34 ± 4b	9 ± 2c
Populus tremuloides	2 ± 1c	61 ± 4b	89 ± 2a
Other species[4]	7 ± 3ab	5 ± 2a	2 ± 2b
Soil texture (%):[5]			
Sand	11 ± 2a	13 ± 3a	14 ± 2a
Silt	43 ± 2a	40 ± 2a	39 ± 3a
Clay	46 ± 2a	47 ± 3a	46 ± 4a

[1]Continuous soil temperature recorded six times a day using dataloggers from May 2007 to May 2009.
[2]Estimated from soil samples of the forest floor and 0-15 cm mineral layers.
[3]Percent and content of C content lost from forest floor samples incubated at 29°C during 100 days.
[4]Other species include jack pine (*Pinus banksiana* Lamb.) and balsam fir (*Abies balsamea* (L.) Mill.).
[5]Textural analysis performed on the 0-15 cm mineral layer.

Table 3.2 Effect of different environmental variables on soil respiration and its components. *F*-statistics derived from mixed linear models (block and microplot nested within block as random effects).

Effect	R_S		R_H		R_A	
	F	*p*	*F*	*p*	*F*	*p*
Soil temperature	243.45	<0.0001	229.42	<0.0001	30.31	<0.0001
Soil moisture	22.83	<0.0001	22.07	<0.0001	4.11	0.0435
Tree proximity	0.21	ns	4.30	0.0388	1.49	ns
Root content	5.58	0.0185	27.00	<0.0001	0.20	ns
Soil carbon:						
Total C content	25.31	<0.0001	42.85	<0.0001	0.45	ns
Percent of very labile C	99.65	<0.0001	84.15	<0.0001	1.64	ns

Table 3.3 Mean (range) soil CO_2 efflux and soil temperature used to develop temperature-soil respiration models. Data were taken from discrete field measurements between June 2007 to June 2008. Significant differences among stand types are denoted by different letters ($p<0.05$).

Variables	BS (n=7)	MW (n=7)	TA (n=8)
Soil CO_2 efflux (μmol m^{-2} s^{-1}):			
R_S	3.75 (0.78-10.91)b	5.29 (1.32-10.36)a	4.83 (1.92-10.50)a
R_H	3.34 (1.31-9.99)b	4.49 (1.64-8.72)a	4.70 (1.19-10.27)a
Soil temperature (°C)	9.5 (2.2-16.2)c	10.0 (2.8-17.4)b	10.4 (3.7-17.6)a

Table 3.4 Equation parameters for the exponential model of the form $R = ae^{b(T-10)}$, where R is the soil respiration R_S or R_H (μmol CO_2 m^{-2} s^{-1}), a is the soil respiration rate at 10°C, b describes the rate of change in R with a unit change of T, which is the soil temperature at a depth of 5 cm. Q_{10} is the temperature sensitivity of R and can be calculated from b ($Q_{10} = e^{(b*10)}$). All model fits were significant ($p<0.001$). Significant differences among stand types are denoted by different letters ($p<0.05$).

Parameter	BS (n=7)	MW (n=7)	TA (n=8)
R_S:			
a	3.8784 ± 0.3294b	5.2255 ± 0.3294a	4.6559 ± 0.3081ab
b	0.09533 ± 0.007342a	0.07978 ± 0.007342ab	0.07231 ± 0.006869b
Q_{10}	2.61 ± 0.17a	2.23 ± 0.17ab	2.07 ± 0.15b
R_H:			
a	3.4943 ± 0.2982b	4.5032 ± 0.3131a	4.3603 ± 0.2846a
b	0.09725 ± 0.01264a	0.06368 ± 0.01305b	0.06540 ± 0.01200b
Q_{10}	2.70 ± 0.17a	1.94 ± 0.17b	2.04 ± 0.15b

Table 3.5 Mean (± SE) soil CO_2 efflux rate and cumulative soil CO_2 efflux estimated from models. Significant differences among stand types are denoted by different letters ($p<0.05$).

Variables	BS (n=7)	MW (n=7)	TA (n=8)
Soil CO_2 efflux rate (μmol m^{-2} s^{-1}):			
R_S	2.67 ± 0.17b	3.84 ± 0.17a	3.56 ± 0.16a
R_H	2.39 ± 0.12b	3.47 ± 0.12a	3.46 ± 0.11a
R_A[1]	0.39 ± 0.09a	0.41 ± 0.09a	0.29 ± 0.09a
Annual soil CO_2 efflux (g C m^{-2} yr^{-1}):			
R_S	1020 ± 64b	1462 ± 64a	1353 ± 60a
R_H	905 ± 46b	1315 ± 46a	1313 ± 43a
R_A	146 ± 36a	148 ± 36a	56 ± 33b*

[1]Estimated as the difference between R_S and R_H. In some cases where the difference was negative, R_A was considered equal to 0.
*Significant at $p<0.10$.

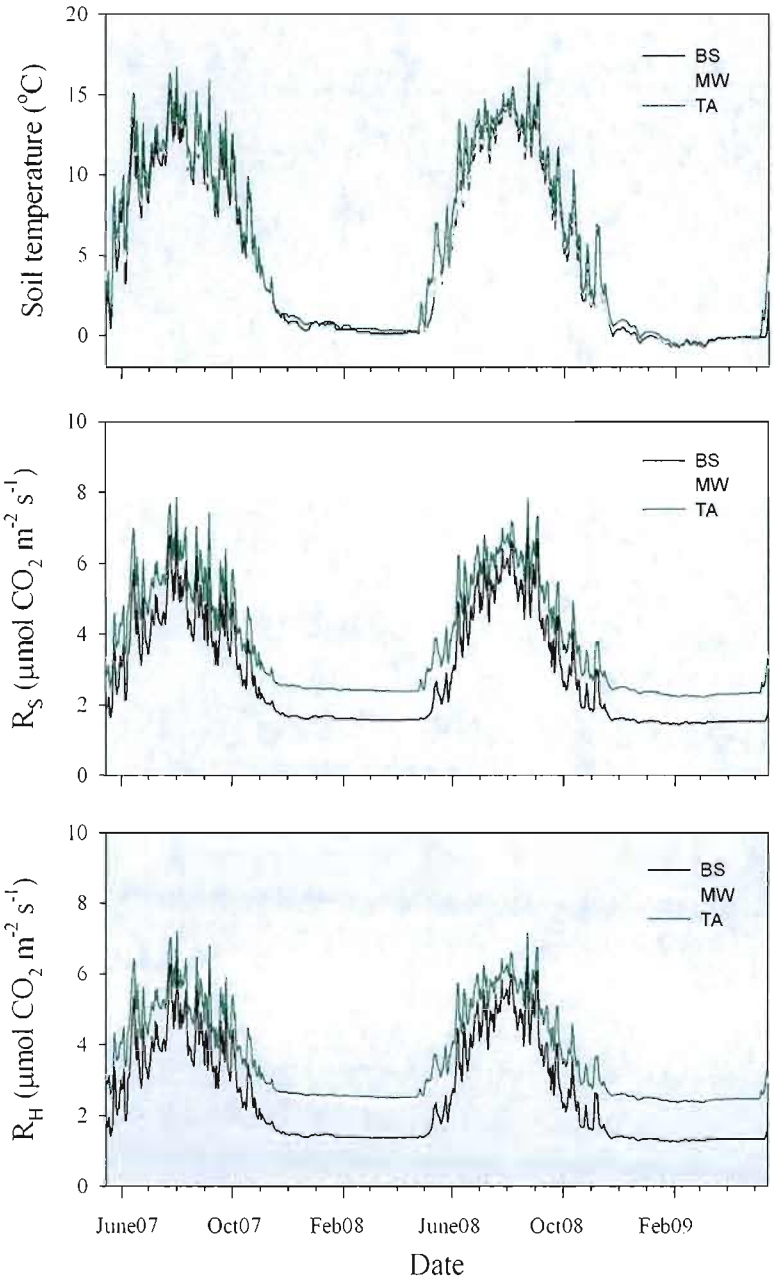

Figure 3.1 Seasonal course of daily mean soil temperature at a depth of 5 cm (upper), and modeled R_S (middle) and R_H (lower).

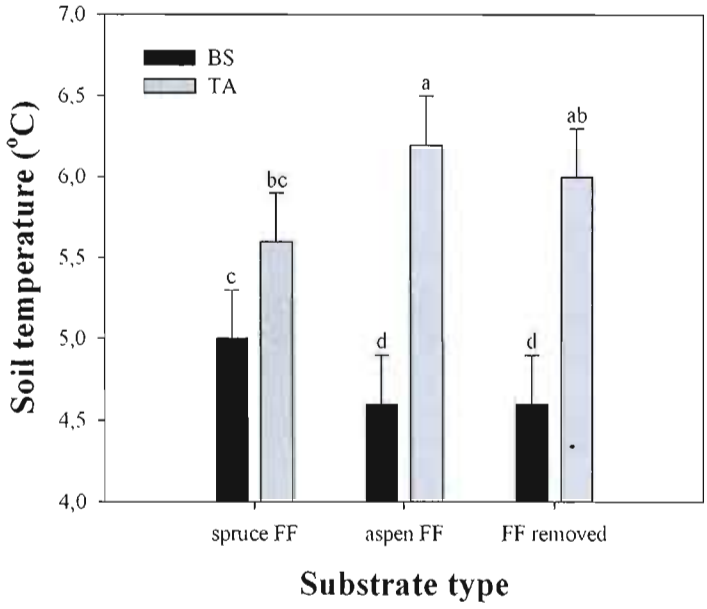

Figure 3.2 Mean annual temperature at a depth of 5 cm in the mineral soil below different substrates transplanted in two single-species stands (BS, black spruce; TA, trembling aspen). FF, forest floor. Significant differences are denoted by different letters ($p<0.05$).

CONCLUSION

Cette étude visait à mieux comprendre l'influence de la composition forestière sur la dynamique du COS dans le Bouclier boréal du Canada. Le premier chapitre avait comme objectif de déterminer la quantité, la distribution verticale et la qualité de COS présent dans différents types de peuplements. Le deuxième chapitre avait comme objectif d'évaluer la répartition du COS dans des fractions physiques de sol qui varient en stabilité. Finalement, le troisième chapitre visait à estimer les pertes annuelles de COS *in situ* et les facteurs responsables de la variation de ces pertes entre les types de peuplements. Collectivement, les résultats de cette thèse ont montré que la composition forestière influençait grandement l'accumulation, le stockage et la libération du COS. Plus spécifiquement, les résultats du Chapitre I ont montré que les forêts contenant du peuplier faux-tremble accumulaient moins de COS en surface que les forêts contenant des conifères (pin gris et épinette noire), mais que le stock de COS du peuplier était plus stable parce qu'il contenait moins de C actif et parce qu'une plus grande partie était située en profondeur, endroit où le C est moins susceptible d'être libéré dans l'atmosphère, comparativement aux autres types de forêts. Les résultats du Chapitre II ont montré que même si les forêts contenant du peuplier accumulaient moins de COS dans le sol minéral de surface, une plus grande part de ce COS était situé dans les fractions physiques du sol les plus stables, c.-à-d. celles étroitement associées aux particules minérales. Enfin, les résultats du Chapitre III ont montré que les forêts d'épinettes noires étaient celles qui avaient les pertes annuelles de CO_2 les moins élevées, mais que ces sols étaient les plus sensibles à l'augmentation de la température de sorte que leur réponse au réchauffement se traduisait par une libération de CO_2 plus élevée par rapport aux autres types de forêts. Ces sols seraient aussi plus susceptibles à perdre du COS suite à des perturbations car le microclimat du sol, plus froid sous l'épinette, est en partie responsable des différences de flux entre les types de forêts. La qualité des apports en C serait un autre facteur important pour expliquer les différences dans les pertes de CO_2 entre les types de forêts étudiées.

Somme toute, le rajeunissement des forêts et notamment l'augmentation du couvert de peuplier faux-tremble dans le paysage canadien diminuerait la taille des stocks de COS, mais en augmenterait la stabilité. Par ailleurs, si les changements climatiques favorisent des conditions d'humidité et de température du sol propice à l'activité des microorganismes, les forêts d'épinettes noires, qui possèdent d'importants stocks de COS et qui dominent la forêt boréale canadienne, pourraient perdre de grandes quantités de COS. Toutefois, l'impact potentiel du réchauffement planétaire sur la dynamique du C dépendra non seulement de la stabilité des stocks de COS face à l'augmentation de la température, mais également de la réponse de facteurs régulateurs pouvant générer une rétroaction négative, affaiblissant par le fait même le réchauffement climatique (Lorenz et Lal 2010). Par exemple, les changements climatiques pourraient provoquer une augmentation de la PPN et/ou une diminution de la décomposabilité de la litière produite, permettant ainsi de compenser pour les pertes additionnelles engendrées par l'augmentation de la décomposition du COS suite à l'augmentation de la température. Cependant, le bilan net de COS suite à ces changements est difficile à prédire et ne fait toujours pas l'objet d'un consensus auprès de la communauté scientifique (Lorenz et Lal 2010). Bien que fort intéressant, ce thème de recherche touchant le bilan complet de COS dans un climat changeant ne faisait pas partie des objectifs du présent ouvrage. Toutefois, un effort de synthèse mobilisant tous les collègues ayant travaillés sur les mêmes sites de recherche, mais sur différentes composantes de l'écosystème (c.-à-d. biomasses aérienne et racinaire), sera effectué prochainement.

La présente thèse constituait un travail pionnier dans le domaine de l'écologie forestière puisque l'étude de l'influence des espèces d'arbres sur le fonctionnement des processus du sol est récente et demeure encore sous-étudiée (Lorenz et Lal 2010). Les résultats issus de cet ouvrage ont permis d'accroître la compréhension du fonctionnement de l'écosystème forestier et sa rétroaction aux changements climatiques. Ce travail a aussi permis l'avancement des connaissances au niveau des associations interspécifiques chez les arbres et notamment de savoir que l'aménagement de forêts mixtes n'accroît pas nécessairement la séquestration du carbone dans les sols du Bouclier boréal bien que des effets non additifs aient été observés. Conjointement, les résultats ont démontré l'importance de considérer l'effet de la composition forestière dans les modèles climatiques. Dans un

contexte d'aménagement durable, il est essentiel d'accroître la recherche visant à comprendre le fonctionnement de la forêt et à prédire sa réponse aux changements climatiques et aux différentes pratiques d'aménagement du territoire.

Naturellement, chaque travail de recherche possède ses limites. Ainsi, les résultats issus du présent ouvrage se limitent aux forêts naturelles dites « productives » du Bouclier boréal du Canada évoluant sur des types de sol similaires à ceux étudiés ici et ne peuvent pas être appliqués notamment aux forêts d'épinette noire peu productives dites « paludifiées » (sensu Lavoie et al. 2005), fréquentes dans la ceinture d'argile. De plus, les résultats observés sont valides seulement pour les peuplements arrivés à la maturité de récolte. En effet, les peuplements à l'étude dans la région de l'Ontario et celle du Québec avaient 85 et 92 ans, respectivement. Les mêmes effets ne sont probablement pas détectables dans les premières années suivant l'établissement du peuplement car l'influence de l'espèce d'arbre (et de sa strate de sous-bois associée) sur le sol n'a pas encore eu le temps de s'exprimer. Par ailleurs, la durée de l'effet observé lorsqu'un peuplement subit une perturbation, comme une coupe forestière ou un feu, n'est pas documentée dans cet ouvrage. Toutefois, sachant que le temps de résidence de certaines formes de carbone dans le sol minéral peut être beaucoup plus long que le temps d'une rotation forestière (von Lützow et al. 2006), l'influence du type de peuplement sur le sol pourrait s'exprimer encore plusieurs années après une perturbation et même après l'établissement d'un peuplement de composition différente, mais la durée de cet effet est inconnue.

La recherche future traitant de l'influence de la composition forestière sur les processus du sol devrait se pencher sur d'autres espèces d'arbres communes à la forêt boréale, notamment le sapin baumier (*Abies balsamea* (L.) Mill.) et le bouleau à papier (*Betula papyrifera* Marsh.), sans oublier les interactions potentielles entre ces espèces et avec celles étudiées dans la présente thèse. Il serait également pertinent d'accorder une place plus importante au rôle des bryophytes (p.ex. mousse et sphaigne) dans la séquestration du COS. L'apport de COS provenant de la mortalité des bryophytes est tel qu'il peut dépasser celui provenant de la chute de feuilles des arbres (Oechel et Van Cleve 1986; Bisbee et al. 2001). Par ailleurs, certaines espèces de sphaigne sont si résistantes à la dégradation microbienne que leur présence dans un peuplement pourrait modifier significativement la dynamique du

COS (Fenton et al. 2010). Parmi les autres aspects, non considérés dans cet ouvrage, qu'il serait intéressant à explorer, figure le rôle du feu dans la séquestration du COS. En effet, nombre d'études ont montré le potentiel de séquestration à long terme du charbon (von Lützow et al. 2006; Jastrow et al. 2007). Sachant que la susceptibilité et la sévérité d'un feu seraient influencées par la composition forestière (Epting et Verbyla 2005; De Deyn et al. 2008), les espèces d'arbres pourraient influencer la séquestration du COS via la quantité et la qualité du charbon présent dans le sol. Enfin, un des sujets chauds actuellement en biologie des changements planétaires et qui mérite attention, concerne le destin des réservoirs de COS stables du biome boréal, puisque la majeure partie du COS total serait protégée contre la décomposition. Un nombre grandissant d'études s'intéressent à la variation de la sensibilité de la décomposition à la température (Q_{10}) en fonction de la qualité de la MOS (protection biochimique ou récalcitrance), tel que discuté dans le Chapitre I, mais peu d'efforts de recherche sont investis pour étudier l'impact du réchauffement et de l'aménagement forestier sur les processus de stabilisation et de déstabilisation du COS protégé chimiquement et physiquement à l'intérieur des agrégats de sol. Sachant qu'environ 85% du COS était protégé à l'intérieur des agrégats de sol dans nos sites (Chapitre II), il serait intéressant de connaître la réaction de ce grand réservoir de COS face aux changements planétaires en cours.

REFERENCES

Abiven, S., S. Menasseri, et C. Chenu. 2009. The effects of organic inputs over time on soil aggregate stability - A literature analysis. Soil Biology and Biochemistry 41: 1-12.

Abu-Hamdeh, N. H., et R. C. Reeder. 2000. Soil thermal conductivity: Effects of density, moisture, salt concentration, and organic matter. Soil Science Society of America Journal 64: 1285-1290.

Aerts, R., et F. S. Chapin. 1999. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Advances in Ecological Research 30: 1-67.

Alriksson, A., et H. M. Eriksson. 1998. Variations in mineral nutrient and C distribution in the soil and vegetation compartments of five temperate tree species in NE Sweden. Forest Ecology and Management 108: 261-273.

Amiro, B. D., A. G. Barr, T. A. Black, H. Iwashita, N. Kljun, J. H. McCaughey, K. Morgenstern, S. Murayama, Z. Nesic, A. L. Orchansky, et N. Saigusa. 2006. Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada. Agricultural and Forest Meteorology 136: 237-251.

Angers, D. A., M. S. Bullock, et G. R. Mehuys. 2007. Aggregate stability to water. *In* Soil sampling and methods of analysis, Second edition. *Édité par* M. R. Carter, et E. G. Gregorich. CRC Press, Boca Raton, FL. pp. 811-820.

Angers, D. A., S. Recous, et C. Aita. 1997. Fate of carbon and nitrogen in water-stable aggregates during decomposition of $^{13}C^{15}N$-labelled wheat straw *in situ*. European Journal of Soil Science 48: 295-300.

Bashkin, M. A., et D. Binkley. 1998. Changes in soil carbon following afforestation in Hawaii. Ecology 79: 828-833.

Berg, B. 2000. Litter decomposition and organic matter turnover in northern forest soils. Forest Ecology and Management 133: 13-22.

Binkley, D. 1995. The influence of tree species on forest soils: processes and patterns. *In* Proceedings of the Trees and Soils Workshop. Special Publication No. 10. *Édité par* D. J. Mead, et I. S. Cornforth. Agronomy Society of New Zealand, Canterbury. pp. 1–33.

Binkley, D., et C. Giardina. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42: 89-106.

Binkley, D., et S. C. Resh. 1999. Rapid changes in soils following *Eucalyptus* afforestation in Hawaii. Soil Science Society of America Journal 63: 222-225.

Binkley, D., et D. Valentine. 1991. Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. Forest Ecology and Management 40: 13-25.

Bisbee, K. E., S. T. Gower, J. M. Norman, et E. V. Nordheim. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia 129: 261-270.

Blanco-Canqui, H., et R. Lal. 2004. Mechanisms of carbon sequestration in soil aggregates. Critical Reviews in Plant Sciences 23: 481-504.

Blanco-Canqui, H., R. Lal, F. Sartori, et R. O. Miller. 2007. Changes in organic carbon and physical properties of soil aggregates under fiber farming. Soil Science 172: 553-564.

Bond-Lamberty, B., S. D. Peckham, D. E. Ahl, et S. T. Gower. 2007. Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature 450: 89-92.

Bond-Lamberty, B., C. Wang, et S. T. Gower. 2004. Contribution of root respiration to soil surface CO_2 flux in a boreal black spruce chronosequence. Tree Physiology 24: 1387-1395.

Borken, W., et F. Beese. 2005. Soil respiration in pure and mixed stands of European beech and Norway spruce following removal of organic horizons. Canadian Journal of Forest Research 35: 2756-2764.

Bossuyt, H., J. Six, et P. F. Hendrix. 2005. Protection of soil carbon by microaggregates within earthworm casts. Soil Biology and Biochemistry 37: 251-258.

Bossuyt, H., J. Six, et P. F. Hendrix. 2006. Interactive effects of functionally different earthworm species on aggregation and incorporation and decomposition of newly added residue carbon. Geoderma 130: 14-25.

Bouwman, A. F., et R. Leemans. 1995. The role of forest soils in the global carbon cycle. *In* Carbon forum and functions in forest soils. *Édité par* W. McFee, et J. M. Kelly. Soil Science Society of America, Madison, WI. pp. 503-525.

Brassard, B. W., H. Y. H. Chen, et Y. Bergeron. 2009. Influence of Environmental Variability on Root Dynamics in Northern Forests. Critical Reviews in Plant Sciences 28: 179 - 197.

Brassard, B. W., H. Y. H. Chen, Y. Bergeron, et D. Paré. 2011. Differences in fine root productivity between mixed- and single-species stands. Functional Ecology 25: 238-246.

Canada's NFI. 2010. Canada's National Forest Inventory: Monitoring the Sustainability of Canada's Forests. Available from http://nfi.nfis.org.

Carter, M. R., D. A. Angers, E. G. Gregorich, et M. A. Bolinder. 2003. Characterizing organic matter retention for surface soils in eastern Canada using density and particle size fractions. Canadian Journal of Soil Science 83: 11-23.

Carter, M. R., et E. G. Gregorich. 2007. Soil sampling and methods of analysis, Second edition. CRC Press, Boca Raton, FL.

Cavard, X., Y. Bergeron, H. Y. H. Chen, et D. Paré. 2010. Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests. Canadian Journal of Forest Research 40: 37-47.

Cavard, X., Y. Bergeron, H. Y. H. Chen, D. Paré, J. Laganière, et B. Brassard. 2011. Competition and facilitation between tree species change with stand development. Oikos, doi: 10.1111/j.1600-0706.2011.19294.x.

Chen, W. J., J. M. Chen, D. T. Price, et J. Cihlar. 2002. Effects of stand age on net primary productivity of boreal black spruce forests in Ontario, Canada. Canadian Journal of Forest Research 32: 833-842.

Christensen, B. T. 2001. Physical fractionation of soil and structural and functional complexity in organic matter turnover. European Journal of Soil Science 52: 345-353.

Cole, V. C., C. Cerri, K. Minami, A. Mosier, N. Rosenberg, et D. Sauerbeck. 1996. Agricultural options for mitigation of greenhouse gas emissions. *In* Climate change 1995: Scientific-technical analyses of impacts, adaptations and mitigation of climate change. *Édité par* R. T. Watson, M. C. Zinyowera, et R. H. Moss. Cambridge University Press, Cambridge, UK. pp. 745-771.

Conant, R. T., P. Dalla-Betta, C. C. Klopatek, et J. M. Klopatek. 2004. Controls on soil respiration in semiarid soils. Soil Biology and Biochemistry 36: 945-951.

Conant, R. T., R. A. Drijber, M. L. Haddix, W. J. Parton, E. A. Paul, A. F. Plante, J. Six, et J. M. Steinweg. 2008. Sensitivity of organic matter decomposition to warming varies with its quality. Global Change Biology 14: 868-877.

Côté, L., S. Brown, D. Paré, J. Fyles, et J. Bauhus. 2000. Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. Soil Biology and Biochemistry 32: 1079-1090.

Craine, J. M., N. Fierer, et K. K. McLauchlan. 2010. Widespread coupling between the rate and temperature sensitivity of organic matter decay. Nature Geoscience 3: 854-857.

Davidson, E. A., et I. A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440: 165-173.

De Deyn, G. B., J. H. C. Cornelissen, et R. D. Bardgett. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecology Letters 11: 516-531.

Environment Canada. 2010. Canadian climate normals or averages 1971-2000. Available from http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html.

Epron, D. 2009. Separating autotrophic and heterotrophic components of soil respiration: lessons learned from trenching and related root-exclusion experiments. *In* Soil carbon dynamics: an integrated methodology. *Édité par* W. L. Kutsch, M. Bahn, et A. Heinemeyer. Cambridge University Press, New York, NY. pp. 157-168.

Epting, J., et D. Verbyla. 2005. Landscape-level interactions of prefire vegetation, burn severity, and postfire vegetation over a 16-year period in interior Alaska. Canadian Journal of Forest Research 35: 1367–1377.

Fang, C., P. Smith, J. B. Moncrieff, et J. U. Smith. 2005. Similar response of labile and resistant soil organic matter pools to changes in temperature. Nature 433: 57-59.

Fenton, N., Y. Bergeron, et D. Paré. 2010. Decomposition rates of bryophytes in managed boreal forests: influence of bryophyte species and forest harvesting. Plant and Soil 336: 499-508.

Fenton, N., N. Lecomte, S. Légaré, et Y. Bergeron. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: Potential factors and management implications. Forest Ecology and Management 213: 151-159.

Fierer, N., J. M. Craine, K. McLauchlan, et J. P. Schimel. 2005. Litter quality and the temperature sensitivity of decomposition. Ecology 86: 320-326.

Finzi, A. C., N. Van Breemen, et C. D. Canham. 1998. Canopy tree–soil interactions within temperate forests: Species effects on soil carbon and nitrogen. Ecological Applications 8: 440-446.

Fissore, C., C. P. Giardina, C. W. Swanston, G. M. King, et R. K. Kolka. 2009. Variable temperature sensitivity of soil organic carbon in North American forests. Global Change Biology 15: 2295-2310.

Flanagan, P. W., et K. Van Cleve. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Canadian Journal of Forest Research 13: 795-817.

Gabriel, C. E., et L. Kellman. 2011. Examining moisture and temperature sensitivity of soil organic matter decomposition in a temperate coniferous forest soil. Biogeosciences Discussions 8: 1369-1409.

Gama-Rodrigues, E. F., P. K. Ramachandran Nair, V. D. Nair, A. C. Gama-Rodrigues, V. C. Baligar, et R. C. R. Machado. 2010. Carbon storage in soil size fractions under two cacao agroforestry systems in Bahia, Brazil. Environmental Management 45: 274-283.

Gartner, T. B., et Z. G. Cardon. 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104: 230-246.

Giardina, C. P., M. G. Ryan, R. M. Hubbard, et D. Binkley. 2001. Tree species and soil textural controls on carbon and nitrogen mineralization rates. Soil Science Society of America Journal 65: 1272-1279.

Gornall, J. L., I. S. Jónsdóttir, S. J. Woodin, et R. Van der Wal. 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153: 931-941.

Gower, S. T., J. G. Isebrands, et D. W. Sheriff. 1995. Carbon allocation and accumulation in conifers. *In* Resource physiology of conifers. *Édité par* W. K. Smith, et T. M. Hinckley. Academic Press, San Diego, CA. pp. 217-254.

Gregorich, E. G., et M. H. Beare. 2007. Physically uncomplexed organic matter. *In* Soil sampling and methods of analysis, Second edition. *Édité par* M. R. Carter, et E. G. Gregorich. CRC Press, Boca Raton, FL. pp. 607-616.

Gregorich, E. G., M. H. Beare, U. F. McKim, et J. O. Skjemstad. 2006. Chemical and biological characteristics of physically uncomplexed organic matter. Soil Science Society of America Journal 70: 975-985.

Grondin, P. 1996. Écologie forestière. *In* Manuel de foresterie. *Édité par* J. Bérard, et M. Côté. Les Presses de l'Université Laval, Québec, QC. pp. 133-278.

Gulde, S., H. Chung, W. Amelung, C. Chang, et J. Six. 2008. Soil carbon saturation controls labile and stable carbon pool dynamics. Soil Science Society of America Journal 72: 605-612.

Halpern, M. T., J. K. Whalen, et C. A. Madramootoo. 2010. Long-term tillage and residue management influences soil carbon and nitrogen dynamics. Soil Science Society of America Journal 74: 1211-1217.

Hanson, P. J., N. T. Edwards, C. T. Garten, et J. A. Andrews. 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. Biogeochemistry 48: 115-146.

Hart, S. A., et H. Y. H. Chen. 2006. Understory vegetation dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25: 381-397.

Hassink, J. 1997. The capacity of soils to preserve organic C and N by their association with clay and silt particles. Plant and Soil 191: 77-87.

Hättenschwiler, S., A. V. Tiunov, et S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology Evolution and Systematics 36: 191-218.

Hendershot, W. H., H. Lalande, et M. Duquette. 2007. Ion exchange and exchangeable cations. *In* Soil sampling and methods of analysis, Second edition. *Édité par* M. R. Carter, et E. G. Gregorich. CRC Press, Boca Raton, FL. pp. 197-206.

Hobbie, S. E., P. B. Reich, J. Oleksyn, M. Ogdahl, R. Zytkowiak, C. Hale, et P. Karolewski. 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87: 2288-2297.

Hodson, M. J., et A. G. Sangster. 1999. Aluminium/silicon interactions in conifers. Journal of Inorganic Biochemistry 76: 89-98.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, et D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75: 3-35.

Ilisson, T., et H. Y. H. Chen. 2009a. The direct regeneration hypothesis in northern forests. Journal of Vegetation Science 20: 735-744.

Ilisson, T., et H. Y. H. Chen. 2009b. Response of six boreal tree species to stand replacing fire and clearcutting. Ecosystems 12: 820-829.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Jandl, R., M. Lindner, L. Vesterdal, B. Bauwens, R. Baritz, F. Hagedorn, D. W. Johnson, K. Minkkinen, et K. A. Byrne. 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137: 253-268.

Jastrow, J. D., J. E. Amonette, et V. L. Bailey. 2007. Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. Climatic Change 80: 5-23.

Jenny, H. 1994. Factors of soil formation. A system of quantitative pedology. Dover Publications, New York, NY.

Jonard, M., F. André, F. Jonard, N. Mouton, P. Procès, et Q. Ponette. 2007. Soil carbon dioxide efflux in pure and mixed stands of oak and beech. Annals of Forest Science 64: 141-150.

Karhu, K., H. Fritze, M. Tuomi, P. Vanhala, P. Spetz, V. Kitunen, et J. Liski. 2010. Temperature sensitivity of organic matter decomposition in two boreal forest soil profiles. Soil Biology and Biochemistry 42: 72-82.

Kelty, M. J. 2006. The role of species mixtures in plantation forestry. Forest Ecology and Management 233: 195-204.

Kroetsch, D., et C. Wang. 2007. Particle size distribution. *In* Soil sampling and methods of analysis, Second edition. *Édité par* M. R. Carter, et E. G. Gregorich. CRC Press, Boca Raton, FL. pp. 713-726.

Kuzyakov, Y. 2006. Sources of CO_2 efflux from soil and review of partitioning methods. Soil Biology and Biochemistry 38: 425-448.

Kuzyakov, Y., et G. Domanski. 2000. Carbon input by plants into the soil. Review. Journal of Plant Nutrition and Soil Science 163: 421-431.

Laganière, J., D. A. Angers, et D. Paré. 2010a. Carbon accumulation in agricultural soils after afforestation: a meta-analysis. Global Change Biology 16: 439-453.

Laganière, J., D. A. Angers, D. Paré, Y. Bergeron, et H. Y. H. Chen. 2011. Black spruce soils accumulate more uncomplexed organic matter than aspen soils. Soil Science Society of America Journal, doi: 10.2136/sssaj2010.0275.

Laganière, J., D. Paré, et R. L. Bradley. 2009. Linking the abundance of aspen with soil faunal communities and rates of belowground processes within single stands of mixed aspen-black spruce. Applied Soil Ecology 41: 19-28.

Laganière, J., D. Paré, et R. L. Bradley. 2010b. How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions. Canadian Journal of Forest Research 40: 465-475.

Laird, D. 2001. Nature of clay-humic complexes in an agricultural soil: II. Scanning electron microscopy analysis. Soil Science Society of America Journal 65: 1419-1425.

Lal, R. 2005. Forest soils and carbon sequestration. Forest Ecology and Management 220: 242-258.

Lang, S. I., J. H. C. Cornelissen, T. Klahn, R. S. P. van Logtestijn, R. Broekman, W. Schweikert, et R. Aerts. 2009. An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. Journal of Ecology 97: 886-900.

Laquerre, S., A. Leduc, et B. D. Harvey. 2009. Increase in canopy aspen in black spruce forests of north-western Quebec after clearcutting. Ecoscience 16: 483-491.

Lavigne, M. B., R. Boutin, R. J. Foster, G. Goodine, P. Y. Bernier, et G. Robitaille. 2003. Soil respiration responses to temperature are controlled more by roots than by decomposition in balsam fir ecosystems. Canadian Journal of Forest Research 33: 1744-1753.

Lavoie, M., D. Paré, N. Fenton, A. Groot, et K. Taylor. 2005. Paludification and management of forested peatlands in Canada: a literature review. Environmental Reviews 13: 21-50.

Légaré, S., Y. Bergeron, et D. Paré. 2005a. Effect of aspen (*Populus tremuloides*) as a companion species on the growth of black spruce (*Picea mariana*) in the southwestern boreal forest of Quebec. Forest Ecology and Management 208: 211-222.

Légaré, S., D. Paré, et Y. Bergeron. 2005b. Influence of aspen on forest floor properties in black spruce-dominated stands. Plant and Soil 275: 207-220.

Li, H. J., J. X. Yan, X. F. Yue, et M. B. Wang. 2008. Significance of soil temperature and moisture for soil respiration in a Chinese mountain area. Agricultural and Forest Meteorology 148: 490-503.

Lin, G., J. R. Ehleringer, P. T. Rygiewicz, Mark G. Johnson, et David T. Tingey. 1999. Elevated CO_2 and temperature impacts on different components of soil CO_2 efflux in Douglas-fir terracosms. Global Change Biology 5: 157-168.

Liski, J., H. Ilvesniemi, A. Mäkelä, et C. J. Westman. 1999. CO_2 emissions from soil in response to climatic warming are overestimated - The decomposition of old soil organic matter is tolerant of temperature. Ambio 28: 171-174.

Litton, C. M., et C. P. Giardina. 2008. Below-ground carbon flux and partitioning: global patterns and response to temperature. Functional Ecology 22: 941-954.

Litton, C. M., J. W. Raich, et M. G. Ryan. 2007. Carbon allocation in forest ecosystems. Global Change Biology 13: 2089-2109.

Lorenz, K., et R. Lal. 2010. Carbon sequestration in forest ecosystems. Springer, Dordrecht, The Netherlands.

Luan, J., S. Liu, J. Wang, X. Zhu, et Z. Shi. 2011. Rhizospheric and heterotrophic respiration of a warm-temperate oak chronosequence in China. Soil Biology and Biochemistry 43: 503-512.

Luo, Y., et X. Zhou. 2006. Soil Respiration and the Environment. Academic Press, London, UK.

Maillard, E., D. Paré, et A. D. Munson. 2010. Soil carbon stocks and carbon stability in a twenty-year-old temperate plantation. Soil Science Society of America Journal 74: 1775-1785.

Man, R. Z., et V. J. Lieffers. 1999. Are mixtures of aspen and white spruce more productive than single species stands? Forestry Chronicle 75: 505-513.

Mellander, P.-E., M. Löfvenius, et H. Laudon. 2007. Climate change impact on snow and soil temperature in boreal Scots pine stands. Climatic Change 85: 179-193.

Messier, C., S. Parent, et Y. Bergeron. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. Journal of Vegetation Science 9: 511-520.

Neff, J. C., J. W. Harden, et G. Gleixner. 2005. Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. Canadian Journal of Forest Research 35: 2178–2187.

Neff, J. C., et D. U. Hooper. 2002. Vegetation and climate controls on potential CO_2, DOC and DON production in northern latitude soils. Global Change Biology 8: 872-884.

O'Connell, K. E. B., S. T. Gower, et J. M. Norman. 2003. Net Ecosystem Production of Two Contrasting Boreal Black Spruce Forest Communities. Ecosystems 6: 248-260.

Oechel, W. C., et K. Van Cleve. 1986. The role of bryophytes in nutrient cycling in the Taiga. *In* Forest ecosystems in the Alaskan taiga. *Édité par* K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck, et C. T. Dyrness. Springer, Berlin, Germany. pp. 121-137.

Paquette, A., et C. Messier. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Global Ecology and Biogeography 20: 170-180.

Paré, D., R. Boutin, G. R. Larocque, et F. Raulier. 2006. Effect of temperature on soil organic matter decomposition in three forest biomes of eastern Canada. Canadian Journal of Soil Science 86: 247-256.

Prescott, C. E., L. M. Zabek, C. L. Staley, et R. Kabzems. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Canadian Journal of Forest Research 30: 1742-1750.

Preston, C. M., J. A. Trofymow, et Canadian Intersite Decomposition Experiment Working Group. 2000. Variability in litter quality and its relationship to litter decay in Canadian forests. Canadian Journal of Botany 78: 1269-1287.

Quideau, S. A., R. C. Graham, O. A. Chadwick, et H. B. Wood. 1998. Organic carbon sequestration under chaparral and pine after four decades of soil development. Geoderma 83: 227-242.

Reich, P. B., J. Oleksyn, J. Modrzynski, P. Mrozinski, S. E. Hobbie, D. M. Eissenstat, J. Chorover, O. A. Chadwick, C. M. Hale, et M. G. Tjoelker. 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecology Letters 8: 811-818.

Reichstein, M., T. Kätterer, O. Andrén, P. Ciais, E. D. Schulze, W. Cramer, D. Papale, et R. Valentini. 2005. Temperature sensitivity of decomposition in relation to soil organic matter pools: critique and outlook. Biogeosciences 2: 317-321.

Rey, A., et P. Jarvis. 2006. Modelling the effect of temperature on carbon mineralization rates across a network of European forest sites (FORCAST). Global Change Biology 12: 1894-1908.

Rumpel, C., et I. Kögel-Knabner. 2011. Deep soil organic matter - a key but poorly understood component of terrestrial C cycle. Plant and Soil 338: 143-158.

Saha, S. K., P. K. Ramachandran Nair, V. D. Nair, et B. M. Kumar. 2010. Carbon storage in relation to soil size-fractions under tropical tree-based land-use systems. Plant and Soil 328: 433-446.

Saiz, G., C. Green, K. Butterbach-Bahl, R. Kiese, V. Avitabile, et E. P. Farrell. 2006. Seasonal and spatial variability of soil respiration in four Sitka spruce stands. Plant and Soil 287: 161-176.

Salomé, C., N. Nunan, V. Pouteau, T. Z. Lerch, et C. Chenu. 2010. Carbon dynamics in topsoil and in subsoil may be controlled by different regulatory mechanisms. Global Change Biology 16: 416-426.

Sarkhot, D. V., E. J. Jokela, et N. B. Comerford. 2008. Surface soil carbon size-density fractions altered by loblolly pine families and forest management intensity for a Spodosol in the southeastern US. Plant and Soil 307: 99-111.

Schimel, D., J. Melillo, H. Q. Tian, A. D. McGuire, D. Kicklighter, T. Kittel, N. Rosenbloom, S. Running, P. Thornton, D. Ojima, W. Parton, R. Kelly, M. Sykes, R.

Neilson, et B. Rizzo. 2000. Contribution of increasing CO_2 and climate to carbon storage by ecosystems in the United States. Science 287: 2004-2006.

Schimel, D. S., J. I. House, K. A. Hibbard, P. Bousquet, P. Ciais, P. Peylin, B. H. Braswell, M. J. Apps, D. Baker, A. Bondeau, J. Canadell, G. Churkina, W. Cramer, A. S. Denning, C. B. Field, P. Friedlingstein, C. Goodale, M. Heimann, R. A. Houghton, J. M. Melillo, B. Moore, D. Murdiyarso, I. Noble, S. W. Pacala, I. C. Prentice, M. R. Raupach, P. J. Rayner, R. J. Scholes, W. L. Steffen, et C. Wirth. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414: 169-172.

Schindlbacher, A., S. Zechmeister-Boltenstern, et R. Jandl. 2009. Carbon losses due to soil warming: do autotrophic and heterotrophic soil respiration respond equally? Global Change Biology 15: 901-913.

Senici, D., H. Y. H. Chen, Y. Bergeron, et D. Cyr. 2010. Spatiotemporal variations of fire frequency in central boreal forest. Ecosystems 13: 1227-1238.

Sims, R. A., H. M. Kersaw, et G. M. Wickware. 1990. The autecology of major tree species in the North Central Region of Ontario. Can.-Ont. forest resource development agreement. COFRDA, report 3302.

Six, J., H. Bossuyt, S. Degryze, et K. Denef. 2004. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. Soil and Tillage Research 79: 7-31.

Six, J., R. T. Conant, E. A. Paul, et K. Paustian. 2002. Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. Plant and Soil 241: 155-176.

Six, J., E. T. Elliott, et K. Paustian. 2000. Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no-tillage agriculture. Soil Biology and Biochemistry 32: 2099-2103.

Soil Classification Working Group. 1998. The Canadian system of soil classification, 3rd edn. Agriculture and Agri-Food Canada, Research Branch, Publication No. 1646.

Soja, A. J., N. M. Tchebakova, N. H. F. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. I. Parfenova, F. S. Chapin III, et P. W. Stackhouse Jr. 2007. Climate-induced boreal forest change: Predictions versus current observations. Global and Planetary Change 56: 274-296.

Steele, S. J., S. T. Gower, J. G. Vogel, et J. M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiology 17: 577-587.

Strong, W. L., et G. H. La Roi. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Canadian Journal of Forest Research 13: 1164-1173.

Subke, J.-A., I. Inglima, et M. Francesca Cotrufo. 2006. Trends and methodological impacts in soil CO_2 efflux partitioning: A metaanalytical review. Global Change Biology 12: 921-943.

Sullivan, P. 2010. Snow distribution, soil temperature and late winter CO_2 efflux from soils near the Arctic treeline in northwest Alaska. Biogeochemistry 99: 65-77.

Tisdall, J. M., et J. M. Oades. 1982. Organic matter and water-stable aggregates in soils. Journal of Soil Science 33: 141–163.

Torn, M. S., S. E. Trumbore, O. A. Chadwick, P. M. Vitousek, et D. M. Hendricks. 1997. Mineral control of soil organic carbon storage and turnover. Nature 389: 170-173.

Trofymow, J. A., T. R. Moore, B. Titus, C. Prescott, I. Morrison, M. Siltanen, S. Smith, J. Fyles, R. Wein, C. Camiré, L. Duschene, L. Kozak, M. Kranabetter, et S. Visser. 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Canadian Journal of Forest Research 32: 789-804.

Trumbore, S. E., O. A. Chadwick, et R. Amundson. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science 272: 393-396.

Van Cleve, K., F. S. Chapin III, P. W. Flanagan, L. A. Viereck, et C. T. Dyrness. 1986. Forest ecosystems in the Alaskan taiga. Springer, Berlin, Germany.

Vesterdal, L., I. K. Schmidt, I. Callesen, L. O. Nilsson, et P. Gundersen. 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. Forest Ecology and Management 255: 35-48.

Vincent, J.-S., et L. Hardy. 1977. L'évolution et l'expansion des lacs glaciers Barlow et Ojibway en territoire québécois. Géographie Physique et Quaternaire 31: 357-372.

Vogel, J. G., et D. W. Valentine. 2005. Small root exclusion collars provide reasonable estimates of root respiration when measured during the growing season of installation. Canadian Journal of Forest Research 35: 2112-2117.

Vogel, J. G., D. W. Valentine, et R. W. Ruess. 2005. Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates. Canadian Journal of Forest Research 35: 161-174.

Vogt, K. A., D. J. Vogt, P. A. Palmiotto, P. Boon, J. O'Hara, et H. Asbjornsen. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant and Soil 187: 159-219.

von Lützow, M., I. Kögel-Knabner, K. Ekschmitt, H. Flessa, G. Guggenberger, E. Matzner, et B. Marschner. 2007. SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms. Soil Biology and Biochemistry 39: 2183-2207.

von Lützow, M., I. Kögel-Knabner, K. Ekschmitt, E. Matzner, G. Guggenberger, B. Marschner, et H. Flessa. 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions - a review. European Journal of Soil Science 57: 426-445.

Wang, B., Y. Jiang, X. Wei, G. Zhao, H. Guo, et X. Bai. 2011a. Effects of forest type, stand age, and altitude on soil respiration in subtropical forests of China. Scandinavian Journal of Forest Research 26: 40-47.

Wang, W., S. Peng, T. Wang, et J. Fang. 2010a. Winter soil CO_2 efflux and its contribution to annual soil respiration in different ecosystems of a forest-steppe ecotone, north China. Soil Biology and Biochemistry 42: 451-458.

Wang, X., Y. Jiang, B. Jia, F. Wang, et G. Zhou. 2010b. Comparison of soil respiration among three temperate forests in Changbai Mountains, China. Canadian Journal of Forest Research 40: 788-795.

Wang, X., J. Zhao, J. Wu, H. Chen, Y. Lin, L. Zhou, et S. Fu. 2011b. Impacts of understory species removal and/or addition on soil respiration in a mixed forest plantation with native species in southern China. Forest Ecology and Management 261: 1053-1060.

Wang, X. L., K. Klinka, H. Y. H. Chen, et L. de Montigny. 2002. Root structure of western hemlock and western redcedar in single- and mixed-species stands. Canadian Journal of Forest Research 32: 997-1004.

Wardle, D. A. 2002. Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton, NJ.

Wardle, D. A., O. Zackrisson, G. Hörnberg, et C. Gallet. 1997. The influence of island area on ecosystem properties. Science 277: 1296-1299.

Wei, W., C. Weile, et W. Shaopeng. 2010. Forest soil respiration and its heterotrophic and autotrophic components: Global patterns and responses to temperature and precipitation. Soil Biology and Biochemistry 42: 1236-1244.

Wetterstedt, J. A. M., T. Persson, et G. I. Ågren. 2010. Temperature sensitivity and substrate quality in soil organic matter decomposition: results of an incubation study with three substrates. Global Change Biology 16: 1806-1819.

Xu, X., Y. Zhou, H. Ruan, Y. Luo, et J. Wang. 2010. Temperature sensitivity increases with soil organic carbon recalcitrance along an elevational gradient in the Wuyi Mountains, China. Soil Biology and Biochemistry 42: 1811-1815.

Yohannes, Y., O. Shibistova, A. Abate, M. Fetene, et G. Guggenberger. 2011. Soil CO_2 efflux in an Afromontane forest of Ethiopia as driven by seasonality and tree species. Forest Ecology and Management 261: 1090-1098.

Zak, D. R., D. F. Grigal, et L. F. Ohmann. 1993. Kinetics of microbial respiration and nitrogen mineralization in Great Lakes forests. Soil Science Society of America Journal 57: 1100-1106.

Zhou, X., S. Q. Wan, et Y. Q. Luo. 2007. Source components and interannual variability of soil CO_2 efflux under experimental warming and clipping in a grassland ecosystem. Global Change Biology 13: 761-775.